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No. 49 1984

PATTERN ANALYSIS IN SAVANNA-WOODLANDS AT NYLSVLEY, SOUTH AFRICA

R.H. WHITTAKER

J.W. MORRIS

and

D. GOODMAN

BOTANICAL RESEARCH INSTITUTE • DEPARTMENT OF AGRICULTURE • REPUBLIC OF SOUTH AFRICA
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by

R.H. WHITTAKER, J.W. MORRIS and D. GOODMAN

Editor: D.J.B. Killick

DEPT. VAN LANDBOU EN VISSERYE
NAVORSINGSINSTITUUT VIR PLANTKUNDE
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BOTANICAL RESEARCH INSTITUTE
DEPT. OF AGRICULTURE AND FISHERIES

ISBN 0 621 08265 1

BOTANICAL RESEARCH INSTITUTE — NAVORSINGSINSTITUUT VIR PLANTKUNDE
DEPARTMENT OF AGRICULTURE — DEPARTEMENT VAN LANDBOU
SOUTH AFRICA — SUID-AFRIKA

1984

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Foreword

Ecological research in southern Africa has in the past tended to be descriptive and broad in scope rather than interpretative and detailed. This was largely due to the primary need for basic information on the composition and distribution of vegetation, often covering large tracts of country. The importance of the broad studies is not in question and they will continue to absorb manpower for many years to come. However, it is perfectly clear that there is a great lack of detailed and experimental ecological research in the RSA, which cannot be justified on economic or any other grounds.

It was, therefore, fortunate that during the Second International Congress of Ecology, held in Jerusalem in 1978, the then Chairman of the Planning Panel of the South African Savanna Ecosystem Project, invited the late Robert H. Whittaker to visit South Africa. The purpose of the visit was to study and gather data on pattern in plant communities in a southern African context and, in particular, to undertake studies on the Nylsvley Ecosystem study site. The technique to be applied had already been used in Australia, Israel and the United States of America and was reported on at the Congress. The invitation was accepted and Dr J.W. Morris, at the time a member of the Botanical Research Institute, joined Prof. Whittaker and L.S. Olsvig-Whittaker in the combined field sampling team consisting of nine persons, which undertook the gathering of field data. The study was a prime example of the co-operative research envisaged for the South African Savanna Ecosystem Project, as is evidenced by the credits under Acknowledgements.

This is the most detailed study of pattern undertaken in South Africa to date and will undoubtedly do much to stimulate interest in this interesting field of study. In addition to the contributions made to the understanding of savanna ecology at a scale of detail not previously attempted, and of the field layer in particular, the expansive discussion of the results is bound to elicit comment and debate for many years to come.

This joint paper is Robert Whittaker's last major contribution to ecology. It is clear from reading the paper that Whittaker, the mentor of and driving force behind the team, drawing on a lifetime of experience, has produced a significant work on plant pattern in an African savanna. It is with great pleasure, therefore, that the Botanical Research Institute is able to publish this paper in the *Memoir* series. We trust that it will receive the attention it deserves.

B. DE WINTER
Director: Botanical Research Institute

Pretoria, March 1984

PLATE 1.—Robert Harding Whittaker (1920–1980)

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Abstract

WHITTAKER, R.H., MORRIS, J.W. & GOODMAN, D. (1984). Pattern analysis in savanna-woodlands at Nylsvley, South Africa. *Mem. bot. Surv. S. Afr.* No. 49, pp. 51.

A primary strip transect of 1 025 m and 5 comparative transects of 200–325 m were sampled in subtropical savannas at the Savanna Ecosystem Project study area, Nylsvley, northern Transvaal. Lists and visually estimated covers of plant species were recorded for the 1-m^2 quadrats along the transects. Supplementary data included stratal cover, tree stand counts, and soil samples along the transects, and standard 1–1 000 m^2 plant diversity samples.

Pattern analysis techniques — including measurements of species contagion and scale, species association, spectral analysis of individual species and cross spectra of pairs, frequency domain principal components analysis, and ordination of the quadrats and species by detrended correspondence analysis — were applied to detect major axes of pattern differentiation, to relate species to these and one another and to estimate pattern diversity as degree of community differentiation along the axes of differentiation.

Measurements of degree and scale of contagion of individual species and of species association, were difficult to interpret and offered little understanding of the community patterns. Correlograms, power spectra, and cross spectra were more effective in recognizing periodic relationships for individual species and pairs of species. With these techniques and frequency domain principal components analysis a rough periodicity could be detected in the 1 025-m transect, with tree patches about every 30 m and with *Burkea* and *Terminalia* tending to alternate with one another in these patches. Ordinations by detrended correspondence analysis were effective in arranging quadrats and species along pattern axes related to soil effects.

For two transects on rocky soils, the major pattern axes appeared to reflect soil depth and soil moisture. For the 1 025-m transect (and two shorter transects) in *Burkea africana* savanna on sandy soils, the first axis was related to woody plant cover and correlated factors, the second axis to soil nutrients; third and higher axes were probably related to local effects of animals. The second, nutrient axis led from quadrats with *Burkea* cover to those with cover of *Terminalia sericea*; these two dominants (and *Acacia* species) differently enrich the soil beneath them in nutrients. Two types of *Acacia* savanna on sandy soils had clear patterns from open to covered quadrats. Patterns on the rocky soils are thus determined primarily by physical characteristics of plant microsites, whereas biological effects of plants and animals determine most of the microsite differentiation and pattern in the sandy-soil *Burkea* and *Acacia* savannas.

The savannas are moderately, but not notably, rich in species — 40–60 species/0.1 ha in the rocky-soil and *Acacia* savannas, to 80–100 species/0.1 ha in the open *Burkea* savannas. Pattern diversities measured along the first ordination axes are not very high — 0.4–1.4 half changes (units of 50% turnover in species composition). The diversity can be interpreted on the basis that the soil pattern represents a mosaic of different microsites, or microhabitats, that support individual plants or are open to occupation by seedlings. Plant species may coexist by population turnover including germination and growth of seedlings in microsites with different properties to which different species are adapted. Biological effects are of major importance for the diversification of microsites in the sandy-soil savannas and some other communities. Microsite theory permits interpretation of the high diversity of plant and animal species in relatively stable natural communities.

Uittreksel

'n Primêre strooktransek van 1 025 x 1 m en vyf soortgelyke transekte van 200–325 m lank is in 'n subtropiese savanne in the savanne-ekosisteemstudiegebied, Nylsvley, in Noord Transvaal gemonster. In elkeen van die opeenvolgende 1 m^2 kwadrate is die plantspesies teenwoordig aangeteken asook hulle kroonbedekking. Bykomstig is ook die totale kroonbedekking vir elke stratum en boomgetalle in elke kwadraat genoteer terwyl grondmonsters langs die transek versamel is en standaard 1–1 000 m^2 plantdiversiteitmonsters opgeneem is.

Patroonanalise-tegnieke waaronder die meting van spesiekontakskakeling en skaal, spesie-assosiasies, spektrale analise van individuele spesies en kruisspektrums van pare, hoofkomponente analise gebaseer of frekwensiedata en die ordening van kwadrate en spesies deur middel van neigingsverwydering ooreenstemmingsanalise (DCA) is gebruik om die hoofasse van patroon differensiasie te bepaal waarmee spesies individueel of onderling vergelyk kon word. Patroondifferensiasie as 'n graad van gemeenskapdifferensiasie langs die asse van differensiasie is geskat.

Die meting van die graad en skaal van kontakskakeling van individuele spesies en van spesie-assosiasies was moeilik om te interpreteer en het min bygedra tot die verklaring van gemeenskappatrone. Korrelogramme, spektraalfunksies en kruisspektrums het in die herkenning van periodiese verwantskappe vir individuele spesies en tussen pare spesies beter resultate gelewer. Deur middel van hierdie tegnieke en hoofkomponente analise kon 'n growwe reëlmatigheid in die 1 025 m transek soos weerspieël deur boomgroepe elke 30 m waarin *Burkea africana* en *Terminalia sericea* neig om mekaar af te wissel waargeneem word. Neigingsverwydering ooreenstemmingsanalise is suksesvol aangewend om kwadrate en spesies langs verskillende asse van patroon wat aan die hand van grondeienskappe verklaar kon word, te rangskik.

In die geval van twee van die transekte in gebiede met 'n klipperige grond word die twee hoofasse van patroon deur gronddiepte en grondvog verklaar. Daarteenoor word die patroon vir die 1 025 m transek (asook twee korter transekte) in die *Burkea africana*-savanne op sanderige grond langs die eerste as deur die kroonbedekking van die houtagtige spesies en gekorreleerde faktore en langs die tweede as deur grondnutriënte verklaar. Die derde en daaropvolgende asse se patroon is waarskynlik 'n weerspieëling van die lokale invloed van diere. Die tweede grondnutriëntas word gekenmerk deur 'n hoë bedekking van *Burkea africana* aan die een kant en *Terminalia sericea* aan die anderkant. Die grond onder die genoemde bome (asook onder *Acacia* spp.) word verskillend deur diè bome verryk. Twee van die *Acacia* spp. savannes op sanderige grond het 'n duidelike patroon van oop tot geslote kwadrate getoon. Die plantegroeipatroon vir die klipperige gronde word primêr deur die fisiese eienskappe van die mikro-omgewing bepaal terwyl die differensiasie in mikro-omgewing en die patroon in die *Burkea*- en *Acacia*-savannes op die sandgronde hoofsaaklik deur die biologiese invloede van die plante en diere bepaal word.

Die savannes is matig maar nie opvallend ryk aan spesies nie met 40–60 spesies per 0.1 ha op die klipperige gronde en *Acacia* spp.-savannes en 80–100 spesies per 0.1 ha in die oop *Burkea*-savanne. Die patroondiversiteit langs die eerste as van ordening is nie baie hoog nie — 0.4–1.4 gehalveerde veranderinge (eenheid van 50% omkeer in spesiesamestelling). Die diversiteit kan dus geinterpreteer word dat die grondpatroon 'n mosaïek van verskillende mikroterreine of mikrohabitatte verteenwoordig gekenmerk deur individuele spesies, of is onbewoon en beskikbaar vir saailinge. Plantspesies kan saam voorkom as gevolg van bevolkingsvervanging (verplasing), insluitend kieming en groei van saailinge in mikroterreine met verskillende eienskappe waarby verskillende spesies aangepas is. Biologiese invloede is van besondere belang by die diversifisering van mikroterreine binne die savannes van sanderige gronde en ander gemeenskappe. Die mikroterreinteorie maak die interpretasie van hoë plant en dier spesiediversiteit in relatief stabiele natuurlike gemeenskappe moontlik.

Introduction

Almost all natural communites have patch-like concentrations of species populations, or repeating small-scale gradients of changing species composition, or mosaic-like elements formed by different species, within what we interpret as a single community. Such patterns, and the within-community heterogeneity of habitat that they represent, are important to the niche differentiation and behaviour of species (Usher, 1975; Bratton, 1976a,b; Wiens, 1976; Whittaker *et al.*, 1979a,b) and the relative stability of populations in communities (Smith, 1972; Whittaker & Levin, 1977; Whittaker & Goodman, 1979); and patterns, both stable and successional, are important to the richness of communities (Loucks, 1970; Whittaker & Levin, 1977; Shmida & Whittaker, 1980).

The tradition of pattern analysis in ecology has been concerned primarily with patchiness of individual species, and associations of pairs of species (Cole, 1946, 1949; Greig-Smith, 1952, 1964, 1979; Kershaw, 1957, 1973; Lubke *et al.*, 1976). Ways of applying pattern analysis at commmunity level are needed, if pattern analysis is to contribute effectively to understanding niche relationships, relative stability of species populations, diversity and relative stability of communities. Ordination of small quadrats as an approach to pattern analysis offers promise in this direction (Whittaker *et al.*, 1979a,b; Shmida & Whittaker, 1980; Whittaker & Naveh, 1980). Ordination, approaching patterns through the whole floristic composition of quadrats rather than through species-by-species relations, offers community-level results that are not accessible from traditional techniques. Recently applied techniques of spectral analysis (Platt & Denman, 1975; Ripley, 1978; Whittaker *et al.*, 1979b; Goodman, 1980) also offer new results on patterns with periodic relationships.

At Nylsvley, in the northern Transvaal, the South African National Programme for Environmental Sciences operates a Savanna Ecosystem Project for intensive study of subtropical savannas. The existence of the project — with supporting research facilities, personnel, and knowledge of the savannas — suggested to us an exploration of pattern analysis applied to these communities. A range of techniques including traditional pattern analysis, spectral analysis and frequency domain principal components analysis, and ordination have been applied to test these techniques by comparison and to seek understanding of savanna-woodland patterns. We describe the analyses of six strip transects of lengths from 200 to 1 025 m and suggest implications for the interpretation of community pattern, diversity, and stability.

Study area

The study area is in the Nylsvley Nature Reserve, situated at 24°40'S latitude and 28°43'E longitude and about 200 km north of Pretoria, South Africa — site of the Savanna Ecosystem Project. The Reserve is in a landscape of low relief, with extensive undulating terrain between 1 080 and 1 140 m altitude. The area is underlain by sandstone, grit, and conglomerate bands of the Waterberg System. Outcropping sandstones form Maroelakop, a prominent hill dividing the study area into eastern and western sections. Away from the lithosols of the top and steep sides of Maroelakop, well-drained Hutton Form reddish sandy soils are found with depths of about 2 m (Harmse, 1977). These soils are mostly old, relatively coarse (silt + clay <10%), deeply leached and very nutrient-poor.

Summer temperatures (December and January) at Nylsvley are about 30°C (mean daily maxima) and occasional ground frosts are experienced in winter (June, July and August), when the mean monthly minimum is slightly above 0°C. Mean annual temperatures are around 19°C. The savannas of the area surrounding Nylsvley are generally interpreted as subtropical, for they are continuous with and of the same physiognomy as subtropical savannas farther north (large areas of Zimbabwe, Zambia and the Kruger National Park in the eastern Transvaal, South Africa). The mean annual temperature at Nylsvley and Nylstroom correspond, however, to those in the warm-temperate transition to the subtropical in southern Texas or central Florida. The annual mean of ∿ 19° at Nylsvley may be compared with 22.9°* at Brownsville, Texas and 24.0° at Miami, Florida, U.S. stations representing the northern edge of subtropical climates in the New World. Average annual rainfall at Nylsvley is 630 mm falling on 62 days, mainly from October to March. Further details of climate are given by De Jager & Harrison (1982). Very dry conditions were experienced prior to the sampling reported here. During the 12 months ended January 1979, 76% of the long-term average was recorded while only 162 mm fell during the 3-month, spring period from November 1978 to January 1979, immediately prior to sampling, in comparison with a long-term average of 316 mm for these 3 months.

The dominant vegetation formation is a broadleaf, deciduous, tall woodland with *Burkea africana*, *Terminalia sericea,* and *Ochna pulchra* the principal trees. *Eragrostis pallens* and *Digitaria eriantha* are the dominant grasses in the openings between trees. Patches of leptophyllous thorn woodland, with *Acacia* spp. as dominant, scattered trees, are located within the broadleaf woodland; and Maroelakop is covered by a third type — shorter woodlands with *Barleria bremekampii* and *Diplorhynchus condylocarpon* as dominant woody plants. A phytosociological survey of the whole Nature Reserve has been carried out by Coetzee *et al.* (1976), where further details may be obtained.

The savannas are swept by fire every few years and the vegetation is consequently fire-adapted. Preliminary results on the rich animal communities of the savannas at Nylsvley are summarized by Huntley & Morris (1978). Termite mounds are conspicuous in the patterns of many savannas (Glover *et al.*, 1964; Lawton & Jenik, 1967) and occur in those at Nylsvley. Termite mounds were not, however, a major feature of the savannas sampled and the scattered mounds in these were not crossed by the transects. Significance of termites, dung beetles and other arthropods for community function there is discussed by Huntley & Morris (1978). The Nylsvley Nature Reserve also supports a rich mammalian fauna. Antelopes important as plant consumers include the abundant impala (*Aepyceros melampus*) and smaller numbers of kudu (*Tragelaphus strepsiceros*), gray duiker (*Sylvicapra grimmia*), and steenbok (*Raphicerus campestris*). Although warthog (*Phacochoerus aethiopicus*) are found, the Reserve did not contain elephants or giraffes as consumers of tree foliage.

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* Editor's note: It will be noticed in this memoir that a stop instead of a comma has been used for decimal points and certain words are spelt in the U.S. way e.g. meter for metre etc. Since these features are present in some of the camera-ready material supplied by the authors, they have, for consistency, been retained in the text.

Methods

Transect location and procedure

Six strip transects were taken during January 1979 to represent different phases of savanna-woodland (Coetzee *et al.*, 1976; Huntley, 1977) at Nylsvley. The transects were, so far as homogeneity of the vegetation permitted, linear. Where the transects departed from their primary orientation, individual segments of 50 m were kept as straight as possible to avoid biased sampling. Samples were taken by 4–5 teams of botanists, each team consisting of one or two observers and a recorder, working along the transect tapes; G.K. Theron and J.W. Morris supervised all teams to maintain consistency in plant determinations. Samples were contiguous, 1-m² quadrats along the tapes. In each quadrat visually estimated covers of all vascular plant species were recorded along with total tree, shrub and graminoid cover (and rock cover in transects 4 and 5). Line intercept covers of trees and shrubs were separately recorded along the tapes, and locations, breast-height diameters, and heights of all trees within 5 m on each side of the tape were recorded. Voucher specimens were taken as needed and are deposited at the National Herbarium, Botanical Research Institute, Pretoria, and Cornell University, Ithaca, N.Y.

Transect 1, the principal transect, 1 025 m long, was in a recently burned (September 5, 1978) area of typical *Burkea africana–Eragrostis pallens* savanna. The tape was laid out with north-south orientation, but some segments changed direction at an angle from this to avoid evident vegetational heterogeneity. The terrain is very flat (although very slightly sloping to the north), the soil sandy, and the vegetation visually consistent throughout the kilometer, although the lower (beginning) end of the transect was approaching an open marshy area or vlei.

Transect 2 sampled an adjacent area of the same community, unburned for more than 4 years. The transect, also aimed north-south, extended for 200 m through *Burkea* savanna, with the last part of this showing change in composition toward an *Acacia karroo* patch through which the transect was extended to end at 325 m.

Transect 3 sampled a larger area of *Acacia tortilis–A. nilotica* savanna, also on very flat terrain and probably differing from the *Burkea* savanna in response to soil factors. The transect, 300 m long, was turned in an arc to stay within the homogeneous *Acacia* community.

Transect 4 was on an open, rocky slope of a low, sandstone hill, Maroelakop; the transect, 200 m long, was horizontal and aimed south-east (120°) on an even, north-east-facing slope with an inclination of 10–15°. The vegetation is *Barleria bremekampii–Diplorhynchus condylocarpon* tree woodland in its rocky slope, *Pseudolachnostylis–Diplorhynchus* variation, with *Canthium gilfillanii* dense in the shrub-low tree stratum (Coetzee *et al.*, 1976; Huntley & Morris, 1978).

Transect 5 was on the summit of Maroelakop, 225 m long, aimed west (290° down a gentle slope, south-west facing at 8° inclination, less rocky than transect 4. The vegetation is also part of the *Barleria–Diplorhynchus* woodland grouping on lithosols, being the *Burkea africana –Diplorhynchus* variation with *Loudetia flavida* the dominant grass (Coetzee *et al.*, 1976).

Transect 6, 200 m long, sampled a denser, more mesic phase of *Burkea* woodland near the marsh, or vlei, for which Nylsvley is named. The terrain is flat, the soil sandy but apparently with somewhat more fine particles than in that of transect 1. The transect was aimed north-east, but some segments were at an angle with this to maintain vegetational homogeneity.

Species diversity

Standard 0.1 ha land plant diversity samples (Whittaker *et al.*, 1979a; Naveh & Whittaker, 1980) were taken in all the transect areas. Each diversity sample included tallies of numbers of plant species present in (a) ten contiguous 1-m² quadrats near the middle of the 50-m tape, including both shaded and open quadrats, (b) two, 2 x 5 m areas each containing five of the 1-m² quadrats, (c) a 10 x 10 m area containing the preceding, and (d) the full 20 x 50 m sample. Environmental data, a stand count of all trees, and cover estimates and mean heights of major plant species, or all species, were also recorded. The counts of species numbers in 1 m^2 (mean of 10 samples), 10 m^2 (mean of 2), 100, and 1 000 m^2 were used to calculate the coefficients in the regression: $S = b + d \log A$. (S is species number and A area in m^2; d is the slope of species increment with increasing area, and b a regression-estimated species number for 1 m^2.) The estimated covers for plant species were used to calculate the Simpson index of relative concentration of dominance:

$$C = \sum_{i=1}^{s} p_i^2 = \sum_{i=1}^{s} n_i^2/N^2.$$

(N is total cover of all species, n_i the actual cover and $p_i = n_i/N$ the relative cover of a given species.)

The transects also provide measures of diversity: (a) mean species numbers and dispersions of mean species numbers in m^2 quadrats; (b) the slope of increase in species number from 1 to 10 and 100 m^2 along the transect, in the relation $S = b + d' \log A$—this strip transect d' is different from and larger than the area-based d obtained above; (c) measures of pattern diversity, measured as the extent of change in small-quadrat species composition along axes of pattern differentiation within the community (Whittaker, 1972; Whittaker *et al.*, 1979a,b).

Given the eigenvalues for a quadrat ordination by reciprocal averaging or detrended correspondence analysis (DCA, see next section), pattern diversity in half changes (units of 50% change in species composition) on an axis can be estimated by the relation

$$HC = \sqrt{12EV/(1 - EV)}\,/\,1.349$$

(M.O. Hill, pers. comm.). In DCA (Hill & Gauch, 1980) the axes are scaled in units of mean standard deviation for species distributions; the lengths in SD units of the first, or first and second, axes are then expressions of relative pattern diversity. (Lengths of higher axes are likely to be determined by chance differences in occurrence of species). The HC and SD measures of pattern diversity can differ widely. Ideally length in HC equals 1.349 times that in SD, but with real data the two measures may be closer together than this, or with noisy data the calculated number of SD units may be larger. Pattern diversity was estimated also from the graphical technique of Whittaker (1960) for beta diversity, in which the slope of log sample similarity on sample separation along the ordination axis is extrapolated to zero distance for a similarity of replicate samples (RS), and this with the similarity for extreme samples (ES) is used to calculate beta or pattern diversity in half changes as

$$HC = (\log RS - \log ES)/\log 2.$$

Finally, a new technique of Wilson & Mohler (1980), given a set of samples in proper sequence, estimates a correct spacing of these by similarity measures, measures rates of compositional change between samples, and sums these as a cumulative compositional turnover in half changes along the axis. Wilson & Mohler's (1980) program provides estimates by both the graphical and the cumulative technique. For the present study the program was applied to composite samples, each composite being one-twentieth of the samples in the transect as arranged along the first axis of DCA ordination.

Structure

Vegetation structure was characterized by stratal coverages, stand counts with breast-height diameters and heights of trees, and mean heights for all species. Species have also been classified by growth-forms and life-forms (Table 1 and following tables).

TABLE 1. — Summary of plant forms, abbreviations, and per cents (see text) of 281 species on the list for all transects, Nylsvley savanna-woodlands

A.	*Growth-forms*	
T	Trees	
	Tbd	tree broadleaf deciduous, 8.5%
	Tpl	tree pinnate leguminous, 2.1%
S	Shrubs	
	Sbd	shrub broadleaf deciduous, 6.8%
	Sbe	shrub broadleaf evergreen, 0.7%
	Ssp	shrub spinose deciduous, 0.4%
	Sm	monocot rosette-shrub, 0.7%
	Ssf	shrub suffrutescent (upper parts of stems dying back in unfavorable seasons), 8.9%
	Sv	woody vine or climbing semishrub, 1.8%
H	Herbs	
	Hfd	fern deciduous, 0.4%
	Hgp	graminoid perennial, 18.5%
	Hgas	graminoid summer annual, 2.8%
	Hpd	perennial deciduous forb (excluding graminoid and fern), 23.1%
	Has	summer annual forb, 25.3%
B.	*Life-forms*	
P	Phanerophytes (trees and shrubs)	
	Pmi	microphanerophyte (tree or shrub 2–8 m), 12.8%
	Pn	nanophanerophyte (shrub 25 cm – 2 m), 11.7%
	Pv	woody stemmed liana, 0.7%
C	Chamaephytes (shrubs >25 cm)	
	Csf	semishrub, suffrutescent low shrub (woody at base with herbaceous shoots produced perennially), 2.5%
	Csu	low stem succulent, 2.1%
	Cg	geoxylic suffrutescent, 1.4%
H	Hemicryptophytes (surface-deciduous and evergreen perennial herbs with resting buds that are slightly above the ground)	
	Hsc	scapose or leafy-stemmed erect herb, 27.8%
	Hsp	spreading, prostrate herb, 6.4%
	Hv	twining herb, 1.4%
G	Geophytes (herbs with subterranean meristems)	
	Gb	with bulb, corm, tuber, etc., 6.4%
T	Therophytes (annual herbs)	
	Tsc	scapose or leafy-stemmed annual erect herb, 23.8%
	Tsp	spreading, prostrate annual herb, 1.1%
	Tv	twining annual herb, 1.8%

Growth-forms classify plants by major morphological or structural characters, together with seasonal relations (evergreen or deciduous foliage). Growth-forms overlap and intergrade much more in warm semiarid climates than in temperate forests. Arid-zone perennials often combine several adaptive characteristics including photosynthetic stem, sclerophyllous, or small and short-lived leaves, suffrutescence, succulence, occurrence of spines, and strong-scented unpalatableness. Assignment of species combining these in varied combinations to classes based on one or two characters is necessarily arbitrary. The system used here is based primarily on Whittaker & Niering (1964, 1965). Growth-form and life-form codes are given in Table 1.

The system of life-forms developed by Raunkiaer (1934) classifies plants primarily by the location of the shoot meristematic or embryonic tissue during the unfavorable season, secondarily by other morphological characteristics. Life-forms intergrade continuously from plants with over-wintering meristems protected below the ground surface (geophytes), through those with meristems at the ground surface that are usually somewhat protected by leaf litter or the remains of the previous year's foliage (hemicryptophytes) and those with meristems above the ground surface but below 25 cm (chamaephytes), to those with meristems well above the ground surface fully exposed to climate during the unfavorable season (phanerophytes). Chamaephyte suffrutescents (Csf) or semishrubs, and transitional hemicryptophyte-semishrubs (Hch, Whittaker & Niering, 1965) are common in warm semiarid climates; we have somewhat arbitrarily assigned the hemicryptophyte-semishrubs to either H or Csf. For our area a new class of chamaephytes that are geoxylic suffrutices (Cg) is needed for plants such as *Dichapetalum cymosum, Pygmaeothamnus zeyheri, Elephantorrhiza elephantina,* and *Parinari capensis*. These plants have massive woody structures below ground, in some cases virtually 'underground trees', but appear above ground only as a diffuse patch of suffrutescent terminal branchlets and twigs.

Soil samples

At the same time that the vegetation data were recorded, soil samples were taken along transects 1 and 6 with an auger at 50-m intervals at depths of 0.3–0.5 m. These were air dried, and analysed at Cornell University for particle-size texture, pH, and for nutrient concentrations (by atomic absorption spectrophotometry). Soil depths were determined with an auger at 50-m intervals along transects 1, 3 and 6. Additional soil, litter, and foliage samples were taken from transect 1 (representing *Burkea* cover, *Terminalia* cover, and open phase near 75 and 1 025 m, and *Acacia caffra* cover and open at 325 m), and transect 3 (representing *Acacia tortilis* cover, opening with *Cenchrus ciliaris*, and openings without *C. ciliaris*). For the 2–5 replicates taken in each case, nutrient concentrations in the extractable soil solution and in the air-dried litter and dominant plant foliage were determined.

Multivariate analysis

The primary reliance for the pattern analysis was on ordination of the m^2 quadrats by their species compositions (cf. Whittaker *et al.*, 1979a,b). Ordination can contribute to pattern analysis by showing directions of compositional change in small samples in response to microhabitat gradients. The gradients in question can involve microtopography, small-scale soil differences, shade and other effects of woody plants, and local biological effects such as plant allelopathy and animal disturbance. Ordination, when successful, can reveal directions of compositional response that may not be evident in the field, suggest relative significance of these directions, and scale both samples and species in ways that clarify responses to microenvironmental factors.

All transects were subjected to reciprocal averaging or correspondence analysis (Hill, 1973b, 1974; Gauch, 1977; Gauch *et al.*, 1977), with species occurring in fewer than 5 quadrats deleted and with species covers scaled by octaves (1 = less than 0.5%; 2 = 1%; 3 = 2%; 4 = 3–4%; 5 = 5–8%; 6 = 9–16%; 7 = 17–32%; 8 = 33–64%; 9 = over 64%). However, detrended correspondence analysis (DCA or Decorana), a modification of reciprocal averaging that straightens the first axis and improves the scaling of positions of samples and species on the axes (Hill, 1979a; Hill & Gauch, 1980), proved superior to reciprocal averaging itself and was used as the principal technique. Several versions of DCA were carried out for each transect; these always included ordinations of quadrats with and without the data for tree species, and ordinations with species scores scaled by the maximum cover for any species in the matrix (hence emphasizing dominant species) and scaled by the maximum covers for individual species (hence giving all species equivalent weights). The ordinations normally excluded species with fewer than 5 occurrences and did not use down-weighting of rare species; ordinations using the down-weighting, or excluding species with fewer than 10, or 20 occurrences were also tried in some cases.

The relative consistency of results from ordination variants provides one indication of the strength and significance of the pattern indicated by those ordinations. The axes of reciprocal averaging are scaled from 0 to 100, whereas those of DCA are scaled in SD units of mean standard deviations of species distributions along those axes. The latter units then suggest, along with the eigenvalues, the relative significance of axes. Neither eigenvalues nor SD units are, however, reliable measures of axis significance. Ordinations of randomized data can yield fairly high eigenvalues and SD values.

Comparisons of ordinations of real data, and of the same data randomized, are used as an approach to axis significance. Given a primary matrix of species scores in quadrats, the scores are reassigned at random. (To retain the importance-value structure of the matrix, the scores remain within the rows, representing species, but are given random positions in the columns, representing quadrats). Five replicate randomized matrices were thus produced for a given actual matrix; separate sets of random matrices were prepared for comparison with actual matrices using species cover data, or standardized by species maxima, or standardized by species totals. Actual and randomized matrices were subjected to DCA. Assessments of the significance of axes were based on (a) the ratio of the eigenvalue for a given axis in the DCA of the actual data matrix, to the mean eigenvalue for the 5 DCA's of the corresponding random matrices, and (b) the difference between the eigenvalue for the actual data and the mean eigenvalue for the random data divided by the standard deviation of the five eigenvalues for the random data. The SD values for axis lengths apparently permit no effective comparison of real and randomized data.

The quadrat data were subjected also to numerical classification by two-way indicator species analysis or Twinspan (Hill *et al.*, 1975; Hill, 1979b). Twinspan first arranges the samples by reciprocal averaging, then seeks groups of indicator species that are concentrated in one set of samples and of sparse occurrence in the other. Within the two sets of samples characterized by these species, new sets of indicator species are sought for a second-level division into four sets of samples, and so on. A dichotomous hierarchy of classes of samples determined by species fidelity and characterized by indicator groups of species is thus formed. For pattern analysis, Twinspan can offer an alternative to ordination in seeking groups of samples and species that differ from one another along more than one axis of community differentiation. Composite samples, each the compositional average of a lower-level class or nodum of samples derived from Twinspan, were ordinated by DCA for transect 1. Composite samples for the noda resulting from a simple clustering procedure (Compclus) of Gauch (1979, 1980) also were ordinated. The ordination of composite samples can reduce the influence of noise, or chance difference in small-quadrat composition, in seeking major directions of compositional difference in the community pattern.

Results are not presented for all the multivariate analyses. Numerical classification followed by ordination can be an effective means of finding pattern in complex data (Gauch, 1980), but seemed less useful than DCA ordinations of quadrat data in the present study. Among the variant DCA ordinations tried, those using weighting by species maxima seemed best overall, as judged by subjective criteria and by the comparisons with randomized data. These ordinations, with tree species included, seem to best relate species of all strata to each other and are the basis of most of the figures and tables that follow. Comparable ordinations without tree data are used to test the relation of the pattern axes, when calculated for the undergrowth only, to tree cover.

Other pattern measurements

Species contagion was measured by frequency of presence of species in adjoining pairs of quadrats (Krishna Iyer, 1948; Jones, 1955–56; Greig-Smith, 1964) and an application of block-size tests to running sets of increasing numbers of quadrats (Kershaw, 1957; Greig-Smith, 1964; Hill, 1973a). Scales of contagion (clump diameter) for individual species were sought through peak values of the variance/mean ratio and the Hill (1973a) modification of this — (variance - mean)/mean^2 — and by chi-square comparisons with Poisson distributions. Spacing of species clumps was sought through minimum values of these same measures at distances along the transects up to 50 m. Periodicity of the multispecies patterns was sought by mean similarity values for quadrats separated by increasing numbers of quadrats; the similarity values used were DCA scores on first and second axes, coefficients of community, and percentage similarities for the octave cover values in m^2 quadrats. Species association was measured by the Cole (1949) index, chi-square test of probability of co-occurrence, and percentage similarity of distribution (Whittaker & Fairbanks, 1958; Goodall, 1973, 1978); these measures were used along with the ordinations and Twinspan to look for groups of associated species.

Spectral analysis

One of the purposes of the study was the testing of spectral analysis techniques for the study of pattern in plant communities (see also Ripley, 1978; Whittaker *et al.*, 1979b; Goodman, 1980). Relatively long transects are needed for spectral analysis. Three techniques of time-series analysis were applied to search for repetitive spatial patterns; these were construction of correlograms, calculation of power spectra, and frequency domain principal component analysis. The first two are standard methods, treated at length in Jenkins & Watts (1968); the third is a special technique developed by Wallace & Dickenson (1972) in a meteorological application. Its utility in ecological pattern analysis is explored in Goodman (1980).

The correlogram is a plot of the serial correlation coefficient (autocorrelation) of a single variable against the time-lag, or separation in units along the transect, for which the correlation is calculated. Typically, the serial correlation is fairly high at small lag values and diminishes (approximately geometrically) as lag increases. The decline generally either decreases in slope to approach zero correlation in a roughly asymptotic fashion, or crosses the zero line to show a distinct minimum at a negative value (and then increases to a shallower positive peak at higher lag values). Sometimes further oscillations above and below the zero line occur, with amplitude diminishing as lag increases. The lag at which the serial correlation first crosses or approaches zero is interpreted as reflecting patch size for aggregations of the species in question. The lag corresponding to the next major positive peak estimates the distance between regularly spaced patches. A correlogram asymptotically approaching zero indicates absence of regular patch spacing.

A power spectrum is obtained from the smoothed Fourier transform of the correlogram. The Fourier transform neither adds nor removes information, but merely expresses the correlogram in a different form which will greatly emphasize any tendency for sine-wave-like periodicity in the original data. The smoothing does modify information somewhat by selectively suppressing or distorting the response to certain wavelengths and pattern shapes. Choice of an appropriate smoothing function is a complicated and rather empirical art, although in practice a few standard functions are used, by convention. The power spectrum expresses the amount of variance apportioned to each of a sequence of frequencies (reciprocals of wavelengths) in the original data. Unfortunately, since this method is looking for sinusoidal patterns, interpretations may be problematic when the data contain other sorts of repeated patterns.

Just as cross correlations between two variables may be calculated at various lags, a cross spectrum between two variables may be calculated to indicate the way the covariance between the two is partitioned over various frequencies. When the number of variables is considerable, as is often the case in vegetation analysis, so many cross spectra must be calculated that it is very difficult to abstract any sense of the overall pattern by visual comparison, one pair at a time.

One possible means of resolving a diffuse repeated pattern, involving several species, is through calculating in the frequency domain an analog of conventional principal components. This is accomplished by eigenanalysis of the Hermitian matrix formed of the cross spectra between all pairs of variables at a specified frequency. The resultant eigenvectors describe wave structures (patch structures) at that frequency, in terms of linear combinations of variables taken at respective lags. The eigenvectors are complex, conveying simultaneously an intensity of the contribution of each variable to the aggregate structure as well as the phase relationships among variables in the wave structure.

As in conventional principal component analysis, the wave structures described by separate eigenvectors are orthogonal: the latter exhibit zero coherence at the frequency in question, which is to say they describe wave structures that do not maintain mutually consistent phase relationship. Also, as in principal component analysis, each eigenvalue shows the amount of variance accounted for by its associated eigenvector. Here, this will mean that the amount of variance in the original sequence of all variables, at the specified frequency, which is accounted for by the wave structure described by a particular eigenvector is given by its associated eigenvalue. Finally, the calculation maximizes the variance accounted for by each eigenvector, subject to the orthogonality constraint.

Though the calculation of frequency domain principal components may seem abstruse, it is a mathematically straightforward extension of conventional principal components. The technique does collect together, in a clearly defined fashion, variables which interact to form an aggregate with a repeating spatially distributed pattern. It is consequently a promising technique for community-level analysis. Since the resolution of the aggregates takes place after the frequency of interest has been specified, this program of analysis may be more to the point than the intuitive approach of defining clusters first, by some means that does not consider spatial position or repetition, and then submitting the sequence of cluster scores to spectral analysis in a search for spatial pattern in the clusters. The two approaches could yield quite different results.

The details of the computational techniques in this analysis are the same as in Goodman (1980). The choices of frequencies to examine were suggested by inspection of individual power spectra and selected cross spectra. Throughout the analysis, the cover data were transformed by taking the natural logarithm of the original value plus one. Compared to the untransformed data, this yielded slightly less well-defined peaks in the power spectra, but better-defined peaks in the cross spectra. To avoid the departures from a straight axis in the lower part of transect 1, the analysis and results are for the upper 650 m of that transect. (Similar results were, however, obtained with trial analyses using the full 1 025 m). The curvature of transect 3 compromises its utility for spectral analysis, but the spectra were computed regardless. Spectral analysis was not applied to transect 2, which extended from a *Burkea* into an *Acacia* type.

TABLE 2. — Summarized characteristics of savanna-woodland transects at Nylsvley, northern Transvaal, South Africa

	Acacia savanna		*Burkea* savanna			Maroelakop		All
	3	2b	2a	1	6	4	5	transects
Length, m	300	125	200	1 025	200	200	225	2 275
Stratal coverages								
Trees	26	24	30	30	51	50	29	
Shrubs	0.3	7	3	6	8	18	9	
Graminoids	43	26	29	13	23	10	47	
Forbs	14	5	3	6	4	9	2	
Rock						60	3.5	
Growth-forms, species numbers								
Tree, broadleaf deciduous	2	5	7	17	10	9	12	24
Tree, pinnate leguminous	3	4	1	2	1	2	2	7
Shrub, broadleaf deciduous	2	4	8	12	5	8	7	20
Shrub, broadleaf evergreen		1	1	1	1			2
Shrub, monocot rosette		2	1	1	1	2	2	2
Shrub, suffrutescent	9	7	6	20	11	8	12	25
Vine, woody or suffrutescent	2	1	2	1	1	1	2	5
Total woody	18	24	26	54	30	30	37	85
Herb, fern deciduous						1	1	1
Herb, graminoid perennial	12	25	32	45	23	10	23	52
Herb, graminoid annual		5	4	5	1	2	2	8
Herb, perennial deciduous forb	8	9	17	45	23	9	17	65
Herb, annual forb	22	33	31	60	21	19	26	71
Total herbaceous	42	72	84	155	68	41	69	197
Total species	60	96	110	209	98	71	106	281
Life-forms, species numbers								
Microphanerophyte	5	9	10	24	13	12	17	37
Nanophanerophyte	8	11	11	19	13	11	16	35
Chamaephyte, semishrub	4	3	2	7	2	3	2	7
Chamaephyte, succulent	1	1	1	3		2	2	6
Chamaephyte, geoxylic	1		3	4	4	1	1	4
Hemicryptophyte, erect	15	29	41	57	34	16	29	78
Hemicryptophyte, spreading or twining	4	3	3	18	5	4	6	22
Geophyte, bulb, etc.		2	4	12	5	3	6	18
Therophyte	22	38	35	65	22	19	27	75
Species diversity								
Mean species per m^2								
Woody	0.7	1.9	1.8	2.0	2.7	3.1	2.7	
Perennial herb	3.0	3.5	5.9	3.7	3.1	1.8	5.4	
Annual	1.5	2.5	2.4	6.3	2.4	1.7	2.3	
Total	5.2	8.9	10.1	12.0	8.2	6.6	10.4	
Transect slope index, d' (1–100 m)	17.3	42.1	37.4	42.6	29.2	23.6	32.4	
Simpson index by cover C	0.241	0.094	0.152	0.124	0.180	0.146	0.076	
Mean species per 100-m strip	40	93	85	97	66	54	75	
Pattern diversity measures								
HC, from eigenvalues, 1st axis	2.49	3.30	2.96	2.13	2.95	2.76	2.44	
HC, from eigenvalues, 2nd axis	1.25	2.51	2.21	1.92	1.98	2.17	2.04	
SD units, DCA 1st axis	3.19	4.99	4.66	4.11	4.17	3.63	4.92	
SD units, DCA 2nd axis	1.99	4.73	3.85	3.71	3.38	3.55	4.10	
HC, graphic estimate, 1st axis	1.40	1.02	0.79	0.65	0.38	0.46	0.54	
HC, cumulative calculation, 1st axis	1.32	1.10	0.57	0.67	0.32	0.38	0.65	

Results

Structure and diversity

The vegetation at Nylsvley, like much other African savanna, is not savanna in a common sense — a tropical grassland with scattered individual trees, or without such trees. Physiognomically these are woodlands ranging from fairly open (transects 1, 2a and 3) to moderately dense (transect 4) cover. Structure is horizontally and vertically complex in the *Burkea* savannas: tree species of different heights grow alone and variously combined in clumps, with and without shrub understories; shrub patches and individual shrubs also occur in the open areas, which vary widely in size, density of plant cover, and relative contribution of graminoids, forbs, and geoxylic suffrutescents to that cover. The *Acacia* savannas include shrubs but are more nearly two-layer communities of grass and scattered (but not widely scattered) trees. We follow African practice in terming at least the more open of these communities as savanna (Coetzee *et al.*, 1976; Huntley, 1977), but their complexity of structure affects much of the pattern analysis that follows.

Table 2 gives data on structure and diversity of the transects. Tree stratum coverage ranges from about 25% in *Acacia* (transects 3 and 2b) and 30% in open *Burkea* savannas (transects 1 and 2a), to about 50% in the dense *Burkea* and rocky-slope woodlands (transects 4 and 6). Tree coverages are in the range of other temperate (Whittaker & Niering, 1965) and tropical (Eiten, 1972) woodlands. Shrub cover is moderate in all the communities. Graminoid cover is high in the *Acacia* stands and transect 5, moderate in the *Burkea* savannas, and low in the rocky-slope woodland of transect 4. Graminoid cover is low in the recently burned *Burkea* savanna (13%, transect 1) compared with the unburned sample (29%, transect 2a); the effect is primarily reduction of area of foliage, not killing of graminoid clumps by fire. The non-*Acacia* types lack definite canopy heights; multiple woody layers, not clearly separable from one another, include widely scattered large trees (largest individuals are *Burkea africana, Combretum zeyheri,* and *Dombeya rotundifolia*), through *Terminalia sericea* and other trees of somewhat lower stature, to small tree species (*Ochna pulchra, Lannea discolor*, etc.) and shrubs of varying heights as indicated in the transect tables.

Importances and diameter distributions of the major trees are indicated in the stand summaries, Table 3. Basal areas are in the range characteristic of woodlands (e.g. Whittaker & Niering, 1975), even in the relatively dense rocky-slope stand of transect 4. Upper and lower halves of transect 1 are given separately in Table 3. All the important tree species (except *Combretum zeyheri*) occur throughout the length of the transect, but there is a shift in composition from stronger representation of *Burkea* (with *Ochna* and *Dombeya*) in the upper part toward a larger fraction of *Terminalia* (with *C. zeyheri*) in the lower part of the transect. Heights of the trees forming the upper strata of the *Burkea* savannas are mostly 4–8 m, with scattered taller individuals. *Ochna* grows in coppice-like patches of individuals 1.5–3 m in height and 1–6 cm in diameter (the numerous small individuals in Table 3) and fewer, larger individuals in the major tree stratum, 4–8 m. The Acacias are somewhat smaller, with heights mostly 3–5 m.

Representation of growth-forms and life-forms in Table 2 shows the preponderance of herbaceous over woody species in all the samples. Annual forbs are the largest growth-form group in most of the samples, followed by perennial forbs and (especially in the *Acacia* samples) perennial graminoids. The life-form spectrum for the flora of all transects together is: phanerophytes 75.3%, chamaephytes 6.0%, hemicryptophytes 35.6%, geophytes 6.4%, therophytes 26.7%. The high proportion of hemicryptophyte and therophyte species expresses the concentration of the flora in the lower strata in a semiarid climate. Height relations of the flora are differently expressed in Fig. 1. The frequencies of species in height octaves suggest an irregular lognormal distribution (cf. Whittaker *et al.*, 1979a) with a geometric mean height of 0.45 m.

Species diversities are summarized at the bottom of Table 2, and in Table 4 for the 1–1 000 m² samples taken along the transects and in two other stands at Kruger National Park. The latter are intended to represent savanna-woodlands in a more clearly subtropical climate. Diversities, measured as vascular plant species per 1 m² and 1 000 m², range from moderately high compared with U.S. plant communities (Whittaker, 1965; Del Moral, 1972; Whittaker & Niering, 1975; Glenn-Lewin,

TABLE 3. — Stand summaries for savanna-woodlands at Nylsvley, South Africa. Tree counts in 10-m wide strips along transects

	Basal area	Stems in cm diameter classes							
	m^2ha	2–3	4–6	7–10	11–15	16–20	21–25	26–30	>30
Transect 1, *Burkea* savanna, upper half, 0.5 ha									
Burkea africana	2.49	10	14	14	1	3	7	2	5
Ochna pulchra	0.50	182	28	7				1	
Terminalia sericea	0.67	12	9	17	10	2			
Dombeya rotundifolia	0.39	1		3	2	2	2		
Others	0.08	9	1	2		1			
Totals	4.13	214	52	43	13	8	9	3	5
Transect 1, *Burkea* savanna, lower half, 0.5 ha									
Burkea africana	1.84	3	7	9	2	10	5	3	1
Ochna pulchra	0.30	37	8	1	1	2	1		
Terminalia sericea	1.28	35	36	24	9	5			
Dombeya rotundifolia	0.22			1	1	1			
Combretum zeyheri	0.29				1		1		1
Others	0.10	1		1			1		
Totals	4.03	76	51	36	14	18	8	3	3
Transect 2a, unburned *Burkea* savanna, 0.2 ha									
Burkea africana	3.00	2	2	4		2	4	3	2
Ochna pulchra	1.09	73	22	6	8				
Terminalia sericea	1.03	11	7	4	4	1			1
Others	0.13	1				1			
Totals	5.25	87	31	14	12	4	4	3	3
Transect 2b, *Acacia* savanna, 0.125 ha									
Acacia karroo	1.97	15	12	22	5	1			
Terminalia sericea	0.14	2		3					
Others	0.03	5	1						
Totals	2.14	22	13	25	5	1			
Transect 3, *Acacia* savanna, 0.3 ha									
Acacia tortilis	2.63	1	1	5	18	11	3		
Acacia nilotica	1.00			2	7	3	2		
Others	0.04	3	6						
Totals	3.67	4	7	7	25	14	5		
Transect 4, Maroelakop slope, 0.2 ha									
Diplorhynchus condylocarpon	4.18	96	49	58	16	7	1	1	
Lannea discolor	1.48	16	16	36	4				
Combretum apiculatum	1.01	4	5	6	6	3			
Combretum molle	0.32	4	5	7	1				
Canthium gilfillanii	0.15	51	3						
Others	2.71	25	10	8	7	4	3	1	1
Totals	10.48	196	88	115	34	14	4	2	1
Transect 5, Maroelakop summit, 0.2 ha									
Burkea africana	1.86			4	2	7	2	1	
Lannea discolor	0.99	7	17	5	3	2	1		
Dichrostachys cinerea	0.63	7		1	5	2			
Diplorhynchus condylocarpon	0.20	1	2	4	1				
Others	1.09	18	4	10			2	1	
Totals	4.77	33	23	24	11	11	5	2	
Transect 6, denser *Burkea* woodland, 0.2 ha									
Burkea africana	2.78	3	7	7	10	8	4		
Ochna pulchra	1.72	265	56	10	2	1			
Terminalia sericea	2.18	7	13	19	13	5			
Others	0.32	4	6	2	1	1			
Totals	7.00	279	82	38	26	15	4		

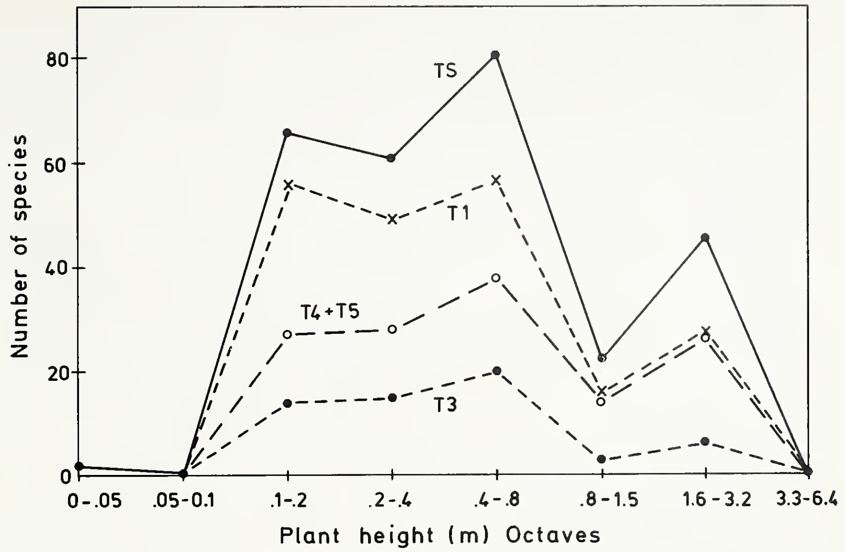

FIG. 1.—Height distributions of species in Nylsvley savanna-woodlands. Numbers of species in octave height classes are plotted for *Acacia* savanna (T3, 60 species), rocky-soil woodlands (T4 and T5, 133 species), the principal transect in *Burkea–Terminalia* savanna (T1, 209 species), and the flora of all transects (TS, 281 species).

1977; Peet, 1978; Golden, 1979) in the *Acacia* communities and rocky-soil woodlands (5–9 spp./m², 40–60 spp./0.1 ha), to high in the open *Burkea* savannas and Kruger National Park (10–13 spp./m², 80–100 spp./0.1 ha). For the latter the slope indices *d*, for addition of species with increasing area, are high—23–29 spp. per 10-fold increase in area. These values are in the range of those for rich Cape Province fynbos (Naveh & Whittaker, 1979). The samples are otherwise moderately, but not notably rich by temperate-zone standards. The richest samples, with 90–100 spp./0.1 ha, are in the same range as some other rich, open, warm-temperate communities —mallee in New South Wales (Whittaker *et al.*, 1979a), mesquite grassland in Texas (Whittaker *et al.*, 1979b), grazed woodlands in Israel (Naveh & Whittaker, 1979) — and some of the Israeli woodlands are richer than any of. our samples. It should be noted, however, that our samples would be somewhat richer in a year more favorable for the annuals. Simpson indices of dominance concentration are mostly low, reflecting mixed dominance in which several major tree and herb species have only moderate coverages.

Pattern diversity represents the degree of compositional change, or species replacement, from one extreme of the pattern to another. It is then a differentiation diversity, analogous to beta diversity (Whittaker, 1977a), and subject to the same kind of measurement in half-change units (number of 50% replacements of species by other species along a compositional gradient). Three pairs of pattern diversity estimates are given on the bottom of Table 2: (a) HC (half-change) estimates calculated from the ordination eigenvalues of the first and second DCA axes, (b) SD (standard deviation) units from the ordinations of samples on the first and second axes, as calculated by DCA, and (c) HC estimates for the first axis only as estimated by graphic and cumulative techniques with the program of Wilson & Mohler (1980). HC and SD units are not the same but may be roughly equivalent for field data (see Methods).

In previous studies of two-phase vegetation with strongly developed open-to-covered axes, the various measures of pattern diversity have been reasonably convergent (Whittaker *et al.*, 1979a,b; Shmida & Whittaker,

TABLE 4. — Savanna–woodland diversity samples, South Africa, 1979. All samples except the last two from the Nylsvley Nature Reserve

Dominants and habitats	Sample no.	Transect no.	Species numbers by areas, m²				Growth-forms S/0.1 ha				Spp-area regression S=b+d log A		Dominance, Simpson
			1	10	100	1000	Tree	Shrub	Per. herb	Ann. herb	b	d	C
Acacia tortilis–A. nilotica	6	3	4.7	9.5	27	46	5	15	13	13	5.9	14.1	0.277
Acacia tortilis–A. nilotica	7	3	6.8	16	37	48	3	18	12	15	5.1	14.5	0.242
Acacia karroo	3	2b	8.9	25	60	62	7	13	20	22	9.6	19.5	0.183
Burkea–Terminalia, unburned	2	2a	12.8	34	65	100	12	25	33	30	8.9	29.3	0.111
Burkea–Terminalia, burned, top	10	1	11.1	26	58	82	12	21	29	20	7.4	24.5	0.146
Burkea–Terminalia, burned, middle	1	1	12.8	39	61	94	6	21	41	26	11.9	26.6	0.108
Burkea–Terminalia, burned, bottom	11	1	7.3	18	36	49	5	11	22	11	5.9	14.4	0.218
Burkea–Terminalia, denser	12	6	8.9	23	43	69	12	15	25	17	5.9	20.0	0.145
Burkea–Lannea, Maroelakop summit	9	5	9.2	23	45	59	13	14	24	8	8.1	17.2	0.165
Diplorhynchus–Lannea, Maroelakop slope	8	4	5.8	15	26	42	10	12	13	7	4.3	12.0	0.372
Combretum zeyheri–C. apiculatum, Kruger National Park	4	–	12.0	33	67	93	4	16	53	20	9.7	27.7	0.100
Combretum zeyheri–Pterocarpus angolensis, Kruger National Park	5	–	10.1	28	53	78	4	10	45	19	8.0	22.9	0.129

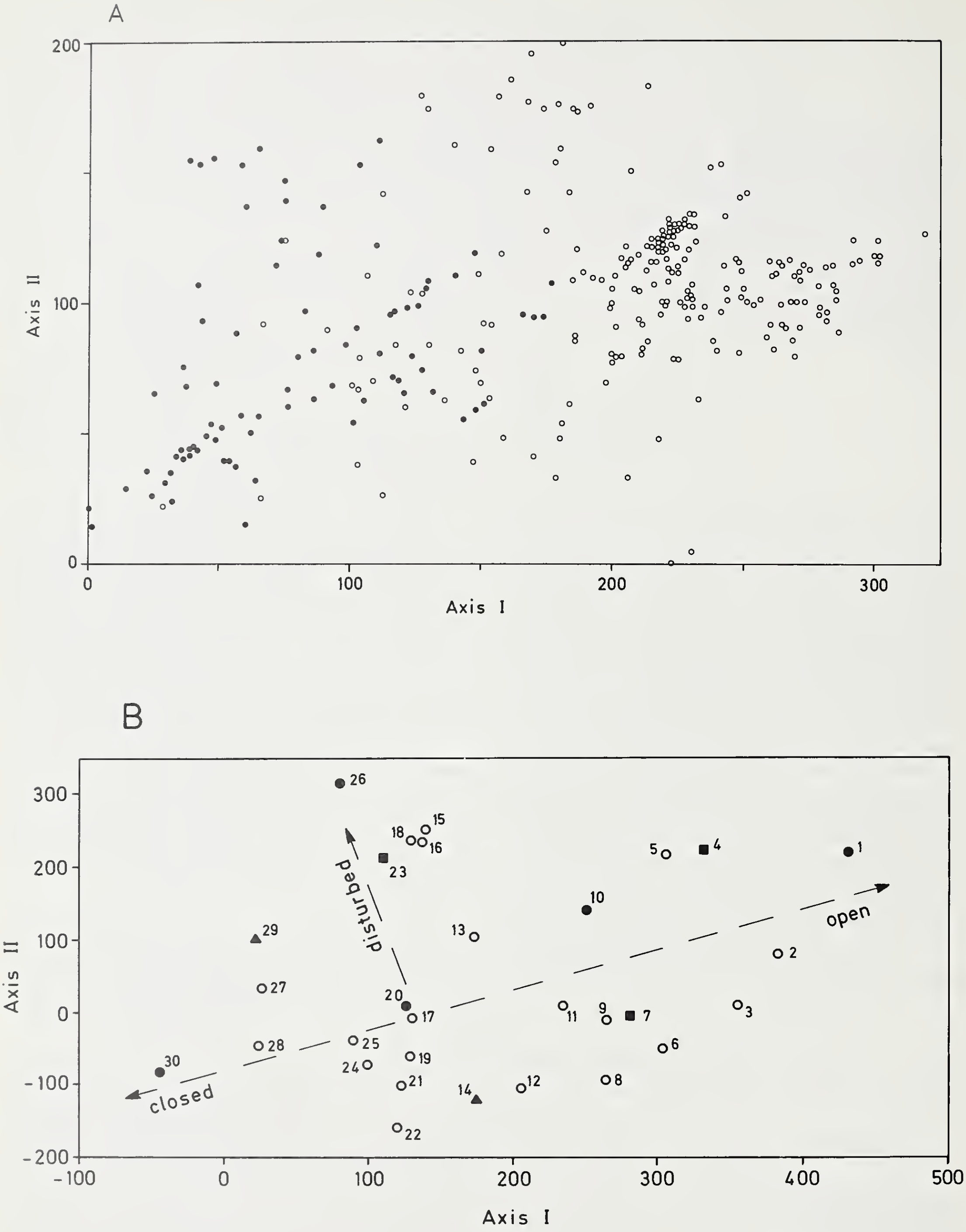

FIG. 2. —Ordination by detrended correspondence analysis (DCA) of transect 3, *Acacia tortilis–A. nilotica* savanna. A, ordination of 300 m² quadrats of the transect. Solid circles represent quadrats with 50% or more tree cover; open circles are for quadrats with less than 50% cover; B, ordination of 30 species; numbers for species are given in Table 5. Growth-form symbols for this and other species ordinations: solid triangles are tree species, solid squares are shrubs, open squares are geoxylic suffrutices; open circles are forbs and solid circles graminoids. Gradients of species response are indicated —*Acacia* cover to openings on axis 1, and toward disturbed sites for the species-group 26, 18, 23, 16, and 15. In DCA the axis length is greater for species than for quadrats, since species with strongly truncated distributions along an axis are given estimated positions beyond the limits of that axis for samples (Hill & Gauch, 1980). In this figure (2B) the second axis has been reduced by one-half relative to the first, to facilitate showing the two charts together.

1980; Whittaker & Naveh, 1980). The divergences of values in Table 2 indicate the difficulties of measuring pattern diversity in these more complex savanna-woodlands with less clearly defined patterns. The eigenvalue estimates of pattern diversity are attractive because they are direct products of the ordination, but they cannot be uncritically accepted. Inspection of actual species turnover in summary tables (e.g., Tables 5–7, 9, 11) indicates that the HC values from eigenvalues overestimate pattern diversity in these transects, while the SD units are more extreme overestimates. In this vegetation the eigenvalue calculations are measuring variance and species turnover that in part represent chance differences in quadrats toward the extremes of the axes. The last two values given in Table 2 are based on 20 composite samples along the first axes of each ordination; and the use of composite samples reduces the effects of chance difference in quadrats to give pattern diversity estimates that are regarded as reasonable, though possibly low.

The pattern diversity estimates indicate: (1) The first-axis pattern diversity is relatively low in these communities, compared with two-phase vegetation giving values of 1.8 to 2.3 on the first axis (Whittaker *et al.*, 1979a,b). However, in communities with strong second axes of differentiation, notably the open *Burkea* savannas, the real pattern diversity values on the first plus second (and possibly higher) axes together may be high; and it is difficult to determine, for calculations paralleling those of the last rows of Table 2 could be carried out on higher axes of decreasing and doubtful significance. (2) Comparing the different transects, the values in the two last rows are effective. Measured pattern diversity, as well as visible differentiation of floras along the open-to-covered axes, decreases from the *Acacia* savannas through the open *Burkea* savannas to the rocky-slope woodlands on Maroelakop. Pattern diversity is lowest, however, in the denser *Burkea* woodland of transect 6.

Pattern in *Acacia* savannas

Ordination

Open *Acacia* savanna or woodland was sampled with two transects — a 300 m strip in a stand dominated by *Acacia tortilis* with *A. nilotica*, transect 3, and the last 125 m of transect 2, dominated by *Acacia karroo*. Both *Acacia* strips were subjected to several ordinations, including reciprocal averaging and DCA, the latter with different data transformations and with trees included in or excluded from the calculations.

The two *Acacia* species of transect 3 occur in clumps that are mostly mixed (with *A. nilotica* subordinate) and that alternate with the grassy open phase of the community. The first series of analyses of transect 3 treated cover of the two Acacias together as a composite variable, to which the other species as variables were related. Results of different ordinations on this basis were similar, though with minor shifts in the sequences of species. The ordination including trees, scaled by matrix maximum, omitting species with fewer than 5 occurrences is illustrated in Fig. 2. In this (and the parallel ordination without trees) the first axis is a clear gradient from quadrats located under trees, primarily *A. tortilis*, to quadrats in the open. The shorter second axis (eigenvalue 0.192 vs 0.484 for the first axis, ordination with trees) separates the tree-covered quadrats from a more limited number of open quadrats. Profiles for first axis scores and for 4 species along the field transect axis are plotted in Fig. 3.

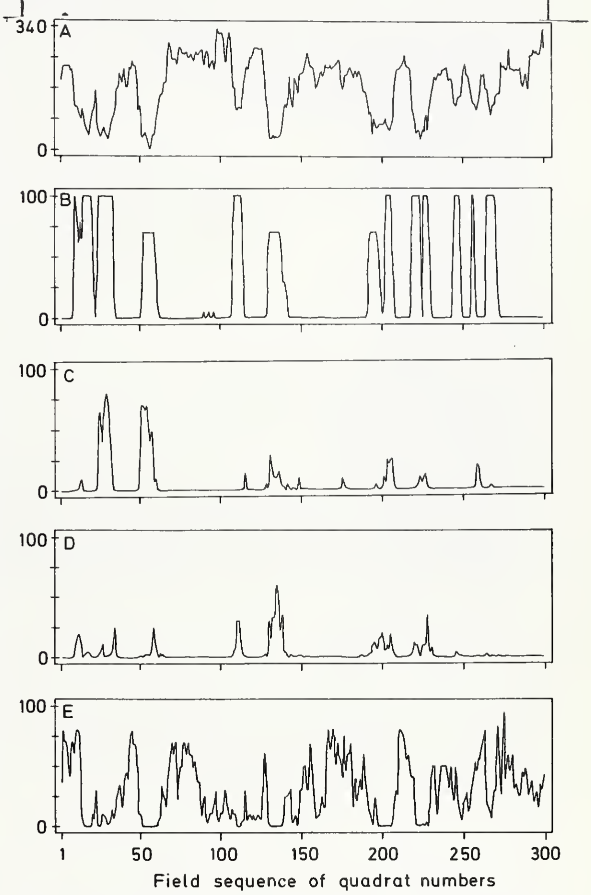

FIG. 3. —Traces of ordination and species scores along the field-sequence of 300, 1-m^2 quadrats of transect 3, *Acacia tortilis–A. nilotica* savanna. A, top-quadrat scores on the first DCA axis, from low scores for covered to high for open quadrats. B, per cent cover for *Acacia* spp. in quadrats as recorded in the field. C, *Panicum maximum* and D, *Achyranthes aspera*, cover per cents for two species with distributions centered under *Acacia*. E, cover per cent for *Eragrostis lehmanniana*, the dominant grass of the openings.

Species characterizations and distributions in 10 sets of 30 quadrats as arranged by first-axis DCA scores are presented in Table 5. At the open end of the first axis the perennial grasses *Heteropogon contortus, Schmidtia pappophoroides* and *Eragrostis lehmanniana* occur with *Evolvulus alsinoides, Talinum caffrum* and *Portulaca quadrifida* as common dicot herbs. These are typical open grassland species of the area, with heights between 0.2 and 1.0 m. The grass *Panicum maximum* and the forbs *Achyranthes aspera, Pollichia campestris, Tagetes minuta* and *Alternanthera pungens* occur in a herb layer about 0.5 m tall under the trees. In this, as in other transects to be described, many species have wide distributions along the first ordination axis (Table 5). Although the trace of DCA scores is irregular (Fig. 3),

TABLE 5. – Species characterization and distribution in an ordination by detrended correspondence analysis (DCA) of transect 3, *Acacia tortilis–Acacia nilotica* savanna

	Species	Transect ranges 1	2	3	4	5	6	7	8	9	10	Score on DCA axis 1 (X 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
		open									closed						
1.	*Heteropogon contortus*	[a]+	+	+	–	+	–	–	+	+	–	[b]431	0.9	[c]21	[d]Hgp	[d]Hsc	[e]0.30/0.8
2.	*Schmidtia pappophoroides*	2	1	+	+	+	+	+	+	–	–	383	3.6	80	Hgp	Hsc	0.20/0.5
3.	*Evolvulus alsinoides*	+	+	+	+	+	+	+	+	–	–	355	0.1	38	Has	Tsc	0.40
4.	*Indigofera daleoides*	+	–	–	–	+	+	+	+	–	–	333		8	Ssf	Pn	0.50
5.	*Talinum caffrum*	+	+	+	+	+	+	+	+	–	–	306	0.1	24	Has	Tsc	0.10
6.	*Leonotis leonurus*	+	–	+	+	+	+	–	–	–	–	304		9	Hpd	Hsc	1.00
7.	*Tephrosia longipes*	–	+	+	+	+	+	+	+	–	–	287		12	Ssf	Pn	0.50
8.	*Portulaca quadrifida*	+	+	+	+	+	+	+	+	–	–	265	0.5	77	Has	Tsc	0.20
9.	*Tribulus zeyheri*	–	+	–	–	+	–	+	–	+	–	265		6	Has	Tsp	0.10
10.	*Eragrostis lehmanniana*	2	4	6	6	4	3	4	2	+	+	251	29.5	192	Hgp	Hsc	0.60/0.9
11.	*Portulaca pilosa*	+	+	+	+	+	+	+	+	+	+	234	0.1	35	Has	Tsc	0.25
12.	*Waltheria indica*	+	+	+	+	+	+	+	+	+	–	207	0.2	21	Hpd	Hsc	0.50
13.	*Solanum panduriforme*	+	1	+	1	1	1	1	1	1	+	173	8.9	285	Hpd	Csf	0.30
14.	*Dichrostachys cinerea*	+	+	–	+	–	+	+	+	+	–	173	0.1	10	Tpl	Pmi	3.00
15.	*Senecio inaequidens*	+	+	–	+	–	+	+	+	+	–	140		12	Hpd	Hsc	0.60
16.	*Conyza bonariensis*	–	+	–	–	–	+	+	+	+	–	138		6	Has	Tsc	0.50
17.	*Commelina erecta*	+	–	–	–	–	–	+	+	–	+	132		7	Has	Tsc	0.15
18.	*Cleome maculata*	–	+	+	–	+	+	+	–	+	+	130		9	Has	Tsc	0.50
19.	*Cyphocarpa angustifolia*	–	–	–	–	+	+	–	+	–	–	129		5	Has	Tsc	0.30
20.	*Aristida congesta* subsp. *congesta*	–	+	+	+	+	+	+	+	+	+	126	1.3	48	Hgp	Hsc	0.25/0.4
21.	*Sida cordifolia*	+	–	–	–	+	+	–	+	+	+	124		9	Has	Tsc	0.40
22.	*Alternanthera pungens*	–	–	+	+	+	+	+	+	+	+	119	0.4	38	Has	Tsc	0.30
23.	*Hermannia quartiniana*	–	+	–	+	–	+	+	+	+	+	110	0.2	19	Ssf	Csf	0.30
24.	*Commelina africana*	–	–	+	+	+	+	+	+	–	+	100		12	Has	Tsc	0.20
25.	*Pollichia campestris*	–	+	–	+	+	+	+	+	+	+	89	0.2	25	Has	Tsc	0.40
26.	*Cenchrus ciliaris*	–	+	+	–	+	+	+	+	1	+	81	3.3	56	Hgp	Hsp	0.30/0.5
27.	*Achyranthes aspera*	–	+	+	–	+	+	+	+	1	1	26	3.3	123	Has	Tsc	0.30
28.	*Tagetes minuta*	–	–	–	–	+	+	+	+	+	+	24	0.1	21	Has	Tsc	0.40
29.	*Acacia* spp.	–	+	+	+	+	+	3	7	9	9	22	25.7	121	Tpl	Pmi	3.00
30.	*Panicum maximum*	–	–	–	–	+	+	+	+	1	3	-44	4.8	81	Hgp	Hsc	0.40/0.8
	Mean number of species per quadrat in composite	4.6	4.8	4.0	3.4	4.0	5.1	5.6	6.3	6.3	5.2						

[a] Table values are deciles of cover, + = presence at less than 10% cover. Each value is an average for a set of 30 samples as ordinated by DCA. 'Transect ranges' are fractions of the samples in ordinated sequence, divided to give equal sample numbers in each range.

[b] Scores are in SD units, based on the mean width (as a standard deviation) of a species distribution along the DCA ordination axis, times 100.

[c] Number of the 300 quadrats in which recorded; not per cent.

[d] For life-form and growth-form code see Table 1.

[e] First mean height given for graminoids is for foliage; height after the slash is for fruiting stems.

change in quadrat composition between adjacent quadrats, as expressed on their first-axis DCA scores, is steep at the edges of the *Acacia* patches relative to that within the patches and the openings. Despite the wide distributions of many species in the pattern, the patches are relatively bordered (cf. Whittaker *et al.*, 1979a,b).

The second ordination axis separates at its high values the grass *Cenchrus ciliaris*, the small forb *Hermannia quartiniana*, and the less common species *Senecio inaequidens* and *Conyza bonariensis*, from the covered quadrats at its low values. The last two species, and to some extent *Cenchrus ciliaris*, are indicators of disturbance (see also Denbow, 1979). The ordinations thus indicate divergences of quadrat composition from tree cover in two directions — toward the normal, prevalent, open grassland of the type dominated by *Eragrostis lehmanniana*, and toward local disturbances within this.

Results of a randomized matrix test are shown in Fig. 4. The first axis for transect 3 seems clearly significant (eigenvalue of 0.484 vs mean eigenvalue and standard deviation of 0.251 ±0.013 for the replicate random matrices). The doubtful significance of the second axis (eigenvalues 0.192 va 0.210 ±0.015) is consistent with its determination by species related to disturbance.

Ordinations in which the two Acacias were treated separately differed in detail from those with the Acacias combined. First axes were again open to closed, but with *A. tortilis* near the closed extreme along with *Panicum maximum* and other species concentrated under the trees. *Acacia nilotica* was separated from *A. tortilis* toward the transition range of the ordination, representing borders of the patches. On the open end of the first axis, the second axis arranged species along what appears to be a successional gradient following disturbance, from earlier (*Leonotis leonurus, Evolvulus alsinoides, Talinum caffrum*, and *Eragrostis lehmanniana*) to later (*Heteropogon contortus, Tribulus zeyheri, Waltheria indica* and *Schmidtia pappophoroides*). Our knowledge of the *Acacia* patch does not permit us to interpret possible history of this apparent gradient, or of the patches with *Cenchrus ciliaris* (which were not on an extreme of the axes in the ordination with both Acacias).

Transect 2 extended through *Burkea* savanna for about 200 m (of which the last part was transitional) into a small patch of *Acacia karroo* savanna. The 125 m² of the *Acacia* phase were ordinated separately by DCA. As in transect 3, the first axis separated covered and open quadrats in ordinations both with and without trees (Fig. 5). In transect 2b, species centered under the

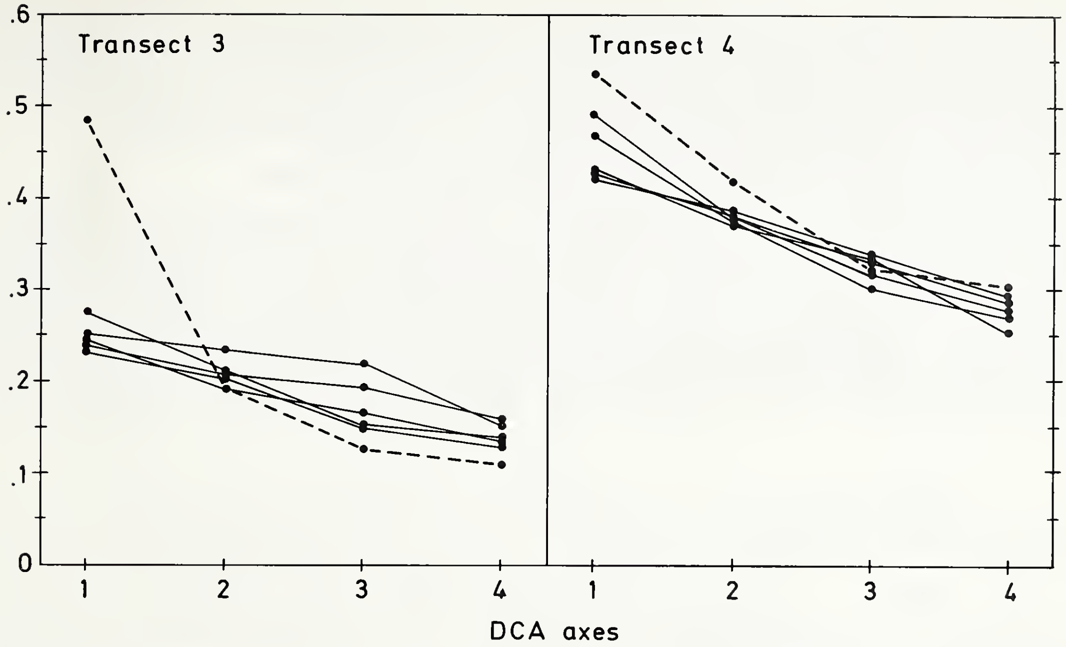

FIG. 4. — Plots of eigenvalues for the first four axes of DCA ordinations of actual quadrat data (heavy dashed lines), vs ordinations of five replicate matrices with species cover values randomly assigned to quadrats (light lines). (All values remain, however, within the rows representing species). The plots provide an indication of the extent to which ordination axes express co-ordinated, directional species responses *versus* merely random difference in quadrat composition. In transect 3 (left) only the first axis and in transect 4 (right) the first and second axes represent significantly co-ordinated species responses.

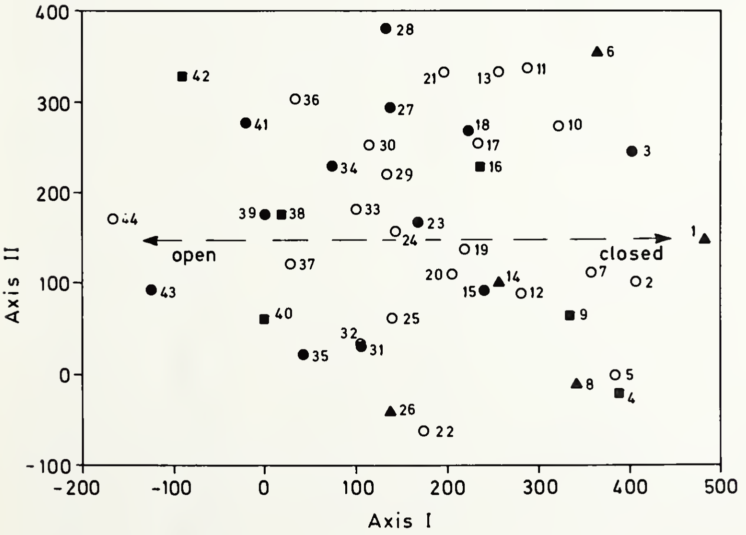

FIG. 5. — Ordination by DCA of 44 species in transect 2b, *Acacia karroo* savanna. Numbers for species are given in Table 6. For growth-form symbols see legend of Fig. 2. Tree species and undergrowth species associated with tree cover are at the right of the ordination field; the remainder represents different phases of the openings.

trees included *Cynodon dactylon, Justicia protracta, Indigofera trita* var. *subulata*, and *Felicia muricata*; species concentrated in the open phase were *Heteropogon contortus, Eragrostis pallens, Indigofera daleoides,* and *Setaria perennis*. Some of these understory species are shared by the two transects (and the *Burkea* savanna as well), but there are marked differences between the two communities beyond their dominance by different species of *Acacia* and grasses (Tables 5 & 6). The contrasts indicate that the two transects sample different phases of *Acacia* savanna. Transect 2b was in a small *Acacia* patch surrounded by *Burkea* savanna, whereas transect 3 was located within a larger, more uniform area of *Acacia*. In the small patch, invasion of *Burkea* savanna species would account for some of its floristic difference from transect 3 and for its stronger floristic link with the *Burkea* savanna. It seems likely, according to the interpretation of Coetzee *et al.* (1976), that the two types represent the effects of a larger area of settlement (transect 3) and a more local old field (transect 2b), both persistent long after abandonment.

Other pattern measurements

Other techniques supported the view of the pattern derived from the ordinations. For transect 3, the search for periodicity (by PS, CC, and DCA score differences for quadrats at increasing distances along the transect) gave a rather weak indication of period at 25 m (mean DCA score difference of 1.055 at 24–25 m, vs background difference of 1.145 at other distances and mean maximum difference, 17–18 and 37–38 m, of 1.252

TABLE 6. — Species characterization and distribution in a DCA ordination of transect 2b, *Acacia karroo* savanna

Species	Transect ranges 1	2	3	4	5	6	7	8	9	10	Score on DCA axis 1 (X 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
	closed ———									——— open						
1. *Acacia tortilis*	[a]6	+	–	–	–	–	–	–	–	–	482	2.2	[b]6	Tpl	Pmi	3.00
2. *Portulaca pilosa*	+	+	+	–	+	–	–	–	–	–	406		6	Has	Tsc	0.25
3. *Cynodon dactylon*	4	2	2	+	+	+		–	–	–	401	3.9	42	Hgp	Hsp	0.10/0.2
4. *Indigofera trita* subsp. *subulata*	+	+	+	+	–	–	–	–	–	–	389	0.1	11	Ssf	Pn	0.50
5. *Justicia protracta*	+	+	+	+	–	+	–	–	–	–	383	0.2	16	Has	Tsc	0.20
6. *Dichrostachys cinerea*	+	2	2	+	+	+	–	+	–	–	364	1.9	8	Tpl	Pmi	3.00
7. *Talinum caffrum*	+	+	–	+	–	–	–	–	–	+	356		7	Has	Tsc	0.10
8. *Rhus leptodictya*	+	–	+	–	+	–	–	–	–	–	341	0.1	6	Tbd	Pmi	3.00
9. *Felicia muricata*	2	3	1	2	2	1	+	+	+	–	332	5.2	73	Ssf	Csf	0.40
10. *Phyllanthus burchellii*	+	+	–	–	+	–	+	+	+	–	323	0.1	11	Has	Tsc	0.20
11. *Blepharis maderaspatensis*	+	+	+	–	+	–	–	–	+	–	286		8	Has	Tsc	0.40
12. *Solanum panduriforme*	+	+	+	+	+	+	+	+	+	+	281	0.2	34	Hpd	Csf	0.30
13. *Rhynchelytrum repens*	–	–	–	+	–	+	–	–	–	–	256	0.2	6	Has	Tsc	0.30/0.6
14. *Acacia karroo*	+	2	2	9	9	4	6	2	1	–	255	14.2	54	Tpl	Pmi	3.00
15. *Schmidtia pappophoroides*	+	+	–	–	+	+	+	+	–	–	240	0.2	10	Hgp	Hsc	0.20/0.5
16. *Ziziphus zeyheriana*	–	+	+	1	+	+	+	–	+	–	232	1.0	11	Ssf	Pn	0.40
17. *Evolvulus alsinoides*	+	+	+	+	+	+	+	+	+	+	232	0.2	43	Has	Tsc	0.40
18. *Eragrostis lehmanniana*	+	+	+	+	+	+	+	+	+	+	224	0.9	48	Hgp	Hsc	0.60/0.9
19. *Pollichia campestris*	–	+	–	+	+	+	+	–	+	–	219	0.5	13	Has	Tsc	0.40
20. *Commelina erecta*	+	+	+	+	+	+	+	+	–	+	204	0.2	25	Has	Tsc	0.15
21. *Dicoma zeyheri*	–	+	+	+	–	+	+	+	+	–	196	0.1	12	Has	Tsc	0.25
22. *Erigeron lehmanniana*	–	–	–	+	+	+	+	+	–	–	174	1.0	18	Has	Tsc	0.30
23. *Digitaria eriantha*	+	+	+	1	+	1	1	1	1	+	169	2.6	92	Hgp	Hsp	0.20/0.35
24. *Eragrostis rigidior*	+	–	+	+	–	+	+	+	+	+	143	0.2	14	Has	Tsc	0.30/0.6
25. *Justicia minima*	–	+	+	–	+	+	+	+	–	+	140	0.1	8	Has	Tsc	0.20
26. *Terminalia sericea*	–	–	–	+	7	+	–	–	1	2	138	4.6	12	Tbd	Pmi	3.00
27. *Stipagrostis uniplumis*	+	+	+	+	+	+	1	1	1	+	137	2.4	36	Hgp	Hsc	0.75/1.0
28. *Aristida congesta* subsp. *congesta*	–	+	+	+	+	+	+	+	+	+	134	0.2	11	Hgp	Hsc	0.25/0.4
29. *Waltheria indica*	–	–	+	+	+	+	+	+	+	+	133	1.0	48	Hpd	Hsc	0.50
30. *Hibiscus pusillus*	+	–	+	–	–	–	+	+	+	+	115			Has	Tsc	0.10
31. *Heteropogon contortus*	–	–	–	+	+	+	+	+	1	+	104	1.7	41	Hgp	Hsc	0.30/0.8
32. *Justicia pallidior*	+	–	–	+	+	+	+	+	+	+	103	0.3	32	Has	Tsc	0.20
33. *Sida cordifolia*	+	–	+	–	–	+	–	+	+	+	100	0.1	9	Has	Tsc	0.
34. *Aristida stipitata*	+	–	+	+	+	+	+	+	+	+	75	0.4	32	Hgp	Hsc	0.30/0.
35. *Eragrostis pallens*	–	–	–	–	+	+	+	+	1	1	42	1.7	25	Hgp	Hsc	0.30/0.9
36. *Cyphocarpa angustifolia*	–	–	–	–	+	–	–	–	+	+	32	0.1	8	Has	Tsc	0.30
37. *Vernonia oligocephala*	–	–	–	+	–	–	–	+	+	+	27	0.1	7	Hpd	Hsc	0.50
38. *Indigofera daleoides*	–	+	–	–	+	+	+	1	+	2	18	2.1	37	Ssf	Pn	0.50
39. *Setaria perennis*	–	–	–	–	1	3	1	+	3	8	0	8.2	38	Hgp	Hsc	0.30/0.6
40. *Diospyros lycioides*	–	–	–	–	–	–	+	3	1	2	-1	3.3	21	Sbe	Pn	1.00
41. *Themeda triandra*	–	–	–	–	–	–	+	+	+	+	-20	0.2	9	Hgp	Hsc	0.60/1.0
42. *Hermannia quartiniana*	–	–	–	–	–	+	–	+	+	+	-92	0.2	11	Ssf	Csf	0.30
43. *Elionurus muticus*	–	–	–	–	–	–	–	–	+	+	-125	0.5	11	Hgp	Hsc	0.30/0.
44. *Rhynchosia longiflora*	–	–	–	–	–	–	–	–	–	+	-168	0.1	7	Hpd	Hv	1.00
Mean number of species per quadrat in composite	7.3	7.4	7.6	9.7	9.5	9.3	8.4	10.2	9.7	9.4						

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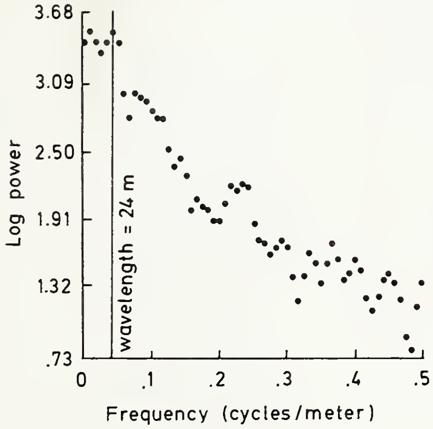
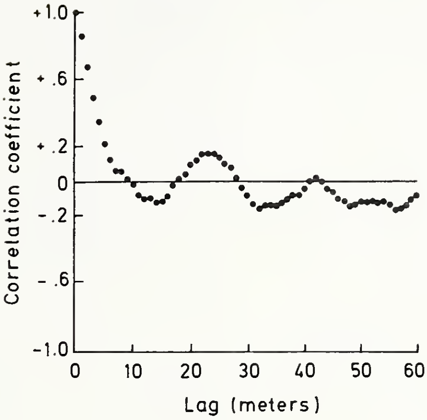
[a] Mean cover deciles in sets of 12 samples as ordinated.

[b] Number of m^2 quadrats in which present out of 120 quadrats in all.

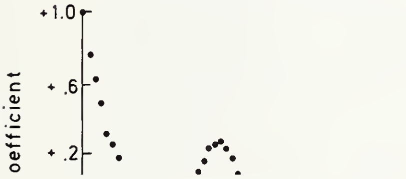
1. Power spectrum, Acacia



2. Correlogram, Acacia



3. Correlogram, Achyranthes



4. Correlogram, Panicum

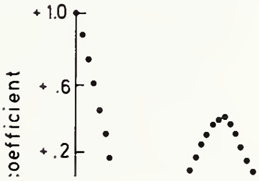


TABLE 7. — Species characterization and distribution in a DCA ordination of transect 1, burned, open *Burkea africana* savanna

Species	Transect ranges																									Score on DCA axis 1 (× 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
	1 closed				5					10					15					20					25 open						
1. *Acacia caffra*	[a]3	+	+	+	+	+	+	+	+	+	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	493	0.7	[b]34	Tpl	Pmi	3.00
2. *Dombeya rotundifolia*	5	1	+	+	+	+	+	–	+	–	+	+	+	–	+	–	–	+	–	–	–	–	–	–	–	460	1.6	37	Tbd	Pmi	2.50
3. *Combretum molle*	1	+	+	+	+	+	–	–	+	+	+	–	–	+	–	–	–	+	–	–	–	–	–	–	–	422	0.5	29	Tbd	Pmi	3.00
4. *Grewia flavescens*	1	+	+	+	+	+	–	+	–	+	+	+	+	–	+	–	+	–	–	–	–	–	–	–	–	417	0.7	37	Sbd	Pn	2.00
5. *Panicum maximum*	+	+	+	–	+	+	+	–	–	–	–	+	+	–	–	+	–	–	–	–	+	–	+	–	–	393	0.1	31	Hgp	Hsc	0.40/0.80
6. *Combretum zeyheri*	1	+	+	+	+	+	+	–	+	–	–	–	+	+	–	–	–	+	–	–	–	+	–	–	–	388	0.5	19	Tbd	Pmi	3.00
7. *Commelina erecta*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	362	0.2	197	Has	Tsc	0.15
8. *Schizachyrium jeffreysii*	+	+	–	+	+	–	+	+	+	+	+	+	+	–	+	–	–	–	–	–	–	–	+	+	+	349	0.1	29	Hgp	Hsc	0.25/0.50
9. *Solanum panduriforme*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	+	+	–	347	0.1	110	Hpd	Csf	0.30
10. *Pentarrhinum insipidum*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	–	337	0.1	107	Has	Tv	0.15
11. *Dichapetalum cymosum*	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	327	0.1	79	Ssf	Cg	0.10
12. *Burkea africana*	3	9	8	9	7	6	8	4	3	3	1	2	1	1	+	+	+	+	+	+	+	+	+	+	–	324	13.1	247	Tbd	Pmi	3.00
13. *Lannea discolor*	+	+	+	+	+	–	+	–	+	+	+	+	+	–	+	+	–	+	–	+	–	–	+	+	–	310	0.3	27	Tbd	Pmi	3.00
14. *Setaria perennis*	1	1	2	1	1	2	1	1	1	1	+	+	1	1	+	1	+	+	+	+	+	+	+	+	+	301	5.0	637	Hgp	Hsc	0.30/0.60
15. *Terminalia sericea*	1	6	6	5	6	6	3	4	6	4	2	1	2	3	+	+	2	1	+	+	+	+	+	+	+	295	11.3	231	Tbd	Pmi	3.00
16. *Phyllanthus burchellii*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	291	0.1	194	Has	Tsc	0.20
17. *Evolvulus alsinoides*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	269	0.1	103	Has	Tsc	0.40
18. *Ochna pulchra*	1	1	1	1	3	1	1	1	1	+	2	1	+	+	1	+	+	1	+	+	+	+	+	+	+	268	4.7	405	Tbd	Pmi	2.50
19. *Commelina africana*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	250	0.1	80	Has	Tsc	0.20
20. *Cyperus sphaerospermus*	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	–	249	0.1	44	Hgp	Hsc	0.10/0.30
21. *Heteropogon contortus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	241	0.4	325	Hgp	Hsc	0.30/0.80
22. *Talinum caffrum*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	237	0.1	92	Has	Tsc	0.10
23. *Themeda triandra*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	235	0.1	106	Hgp	Hsc	0.60/1.00
24. *Mariscus laxiflorus*	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	231	0.1	65	Hgp	Hsc	0.30/0.50
25. *Brachiaria nigropedata*	+	+	+	–	–	–	+	+	–	+	+	+	–	+	+	–	–	–	–	+	–	+	+	+	–	227	0.1	24	Hgp	Hsc	0.30/0.60
26. *Fadogia monticola*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	210	0.6	134	Hpd	Hsc	0.50
27. *Justicia pallidior*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	208	1.1	606	Has	Tsc	0.20
28. *Aristida argentea*	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	205	0.1	86	Hgp	Hsc	0.20/0.60
29. *Vernonia oligocephala*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	200	0.2	161	Hpd	Hsc	0.50
30. *Gisekia pharnaceoides*	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	192	0.1	153	Has	Tsp	0.04
31. *Aristida stipitata*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	187	0.2	135	Hgp	Hsc	0.30/0.90
32. *Digitaria eriantha*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	187	2.1	881	Hgp	Hsp	0.20/0.35
33. *Waltheria indica*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	167	0.3	155	Hpd	Hsc	0.50
34. *Justicia anagalloides*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	163	0.9	571	Has	Tsc	0.20
35. *Lannea edulis*	–	+	+	+	–	–	+	+	+	+	+	+	+	+	+	–	+	–	+	–	+	+	+	–	+	156	0.3	29	Sbd	Pmi	2.50
36. *Urelytrum squarrosum*	–	–	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	141	0.3	90	Hgp	Hsc	0.90/1.50
37. *Justicia minima*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	139	1.0	509	Has	Tsc	0.20
38. *Limeum viscosum*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	124	0.4	584	Has	Tsp	0.10
39. *Cleome maculata*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	108	0.3	610	Has	Tsc	0.50
40. *Indigofera sordida*	+	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	107	0.1	41	Ssf	Csf	0.50
41. *Triumfetta sonderi*	–	+	+	–	+	+	+	–	+	+	+	+	+	–	–	–	+	+	+	+	–	+	+	+	+	100	0.5	31	Ssf	Pn	0.75
42. *Eragrostis pallens*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	99	1.5	669	Hgp	Hsc	0.30/0.90
43. *Diheteropogon amplectens*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	99	0.2	193	Hgp	Hsc	0.80/1.20
44. *Brachiaria serrata*	–	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	93	0.1	86	Hgp	Hsc	0.20/0.50
45. *Pygmaeothamnus zeyheri*	+	–	+	–	–	–	+	+	+	+	+	+	+	–	–	+	–	–	+	+	+	+	+	+	+	93	0.3	30	Ssf	Cg	0.30
46. *Tristachya rehmannii*	–	–	–	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+	78	0.1	51	Hgp	Hsc	1.50/2.00
47. *Elephantorrhiza elephantina*	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	75	0.1	72	Ssf	Cg	0.40
48. *Cyperus margaritaceus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	69	0.3	305	Hgp	Hsc	0.30/0.50
49. *Elionurus muticus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	62	1.1	325	Hgp	Hsc	0.30/0.60
50. *Indigofera daleoides*	–	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	61	0.2	92	Ssf	Pn	0.50
51. *Dicoma anomala*	–	–	–	+	+	–	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	53	0.1	70	Has	Tsc	0.20
52. *Rhynchelytrum setifolium*	–	+	–	+	+	+	+	+	–	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	38	0.1	59	Hgp	Hsc	0.25/0.60
53. *Hypoxis rooperi*	–	–	–	–	–	–	+	+	–	+	+	–	+	+	+	–	+	+	–	–	–	+	–	+	–	22	0.1	13	Hpd	Gb	0.75
54. *Perotis patens*	–	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	11	0.1	97	Hgas	Tsc	0.15/0.30
55. *Fimbristylis hispidula*	–	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	8	0.3	210	Hgp	Hsc	0.20/0.30
56. *Cassia mimosoides*	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6	0.2	172	Hpd	Hsc	0.30
57. *Parinari capensis*	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	-6	0.8	96	Ssf	Cg	0.20
58. *Aristida aequiglumis*	–	+	+	–	–	+	–	–	–	+	+	+	–	+	–	–	+	+	+	+	–	+	+	+	+	-15	0.1	40	Hgp	Hsc	0.20/0.40
59. *Ximenia caffra*	–	–	+	–	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	+	–	+	+	+	-88	0.1	13	Tbd	Pmi	3.00
Mean number of species per quadrat in composite	9.8	12.0	11.4	11.7	11.3	12.1	12.1	12.3	11.5	12.0	11.5	11.8	12.7	12.9	12.4	12.1	11.5	11.6	12.2	11.3	11.2	10.7	11.3	11.8	10.1						

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[a] Mean cover values in deciles, in sets of 41 quadrats as ordinated.
[b] Number of occurrences in the strip of 1 025, 1-m² quadrats.

SD). The test for contagion by frequency of occurrence in adjoining pairs of quadrats gave high probability of contagion for all species occurring in more than 10 quadrats of the 300. Tests for scale of contagion for individual species were, however, weak or nonsignificant. The Hill index gave a weak indication of contagion at 6–7 m for *Acacia* spp. — this scale representing individual trees — whereas the variance/mean ratio gave no peak at that length, but a weak peak at 14–15 m. Peaks of the Hill ratio suggested clump sizes of 5–7 m for *Panicum maximum* and *Achyranthes aspera*, both growing under *Acacia*. Different clump sizes were suggested for species growing in the open — *Eragrostis lehmanniana* (13 m), *Portulaca quadrifida* (5–6 m), and *Schmidtia pappophoroides* (9–10 m). In no species were there troughs in the measures that might indicate spacing of clumps. The tests for species co-occurrence showed positive association of *Acacia* with *Panicum maximum, Achyranthes aspera, Pollichia campestris, Tagetes minuta, Commelina africana*, and *Sida cordifolia*, species related to the *Acacia* cover in the ordinations. Species occurring in the openings — *Solanum panduriforme, Schmidtia pappophoroides, Eragrostis lehmanniana, Portulaca quadrifida* and *Heteropogon contortus* — were related by a less clear pattern of association. Results for the shorter (125 m) strip in *Acacia karroo* woodland gave strong indications of contagion for species represented in more than 12 quadrats, but weak indications of periodicity and in distinct scale of species contagion. A scale of contagion of 8 m was suggested for *Acacia karroo* and is consistent with that of the larger individuals of the species along the transect; for other species the indices gave monotonic slopes or only weak indications of scale that differed for the several indices. These measurements were not particularly informative beyond expressing the rather obvious patches formed by individual *Acacia* trees and their understories.

Spectral analysis

Results consistent with these, but somewhat clearer, were obtained with spectral analysis. Autocorrelations and power spectra were calculated for 12 major species in transect 3, and cross spectra were calculated for each of three species (*Acacia* spp., *Achyranthes aspera* and *Schmidtia pappophoroides*) against all others of these 12. (Spectral analysis was not applied to the shorter strip of transect 2b.) Autocorrelations and power spectra indicated pattern repetition on varying but related scales for the 12 species: 5.5–8 m, 9–14 m, 22–26 m and 39–42 m. Some species showed peaks at more than one of these; peaks near 24 m were most consistent and were strong for three species occurring in the tree clumps — *Acacia* spp., *Achyranthes aspera* and *Panicum maximum* — as shown in correlograms, Fig. 6. The peaks were weak or absent in most species centered in the open (*Eragrostis lehmanniana, Evolvulus alsinoides* and *Portulaca pilosa*) and for species occurring both in the open and under trees (*Solanum panduriforme, Aristida congesta* subsp. *congesta* and *Alternanthera pungens*). One species of the openings, *Schmidtia pappophoroides*, had strong correlogram peaks at 15 and 30 m and a corresponding spectral peak at 17 m wavelength. *Cenchrus ciliaris* showed a weak pattern at 40 m. The only distinct cross spectra occurred in two pairs involving *Acacia*; an in-phase relationship with *Achyranthes aspera* and an out of phase relationship with *Eragrostis lehmanniana*, both showing coherence peaks around 24 m. This scale corresponds to the periodicity of the tree-related clumps; and the phases show *Achyranthes aspera* occurring with *Acacia* in these clumps, whereas the tree clumps alternate with patches in which *Eragrostis lehmanniana* is usually present. For the Acacias and their understory associates, the pattern is clear; in the grassland matrix species are distributed without clear pattern, with *Eragrostis lehmanniana* present throughout and dominant in most of the matrix but replaced locally as dominant by the independent and differently spaced patches of *Schmidtia pappophoroides* or *Cenchrus ciliaris.*

Principal transect: burned *Burkea* savanna

Ordination

A number of DCA ordinations of transect 1 used data scaled by octave covers and by species maxima, with and without downweighting, and with and without rare species; parallel analyses included and excluded the tree species. These multiple, variant ordinations (which gave consistent results with unmistakable shaded-to-open axes in the *Acacia* savannas) at first failed to give an interpretable pattern for transect 1. Variant axes, with widely different species arrangements, difficult to relate to one another and mostly with no clear relation to tree cover, were produced by the variant ordinations. Quadrat clustering (by Compclus; Gauch, 1979) followed by ordination of the clusters as composite samples did not produce a clear pattern but reinforced the impression of complex and haphazard relations among species. Classification by two-way indicator species analysis (Twinspan; Hill, 1979b) also gave no real clarification, although the results of the Twinspan could be interpreted on the basis of the ordination (major Twinspan groupings separated open vs closed, and *Burkea*- vs *Terminalia*-dominated quadrats). Interpretable results of ordination were obtained by: (a) DCA of the full data scaled by species maxima and omitting species occurring in fewer than 10 quadrats (110 species remaining), separate ordinations with and without tree data, and (b) reducing the complexity of the data by separate ordinations of 10 segments of the transect, 100 contiguous quadrats each.

Results of the full DCA ordination of species (1 025 quadrats, scaling by species maxima, no downweighting, species occurring more than 10 times, including trees) are shown in Fig. 7. Axis 1 (EV = 0.407) separates all the tree species (*Ochna pulchra, Burkea africana, Lannea discolor, Combretum molle, Combretum zeyheri, Terminalia sericea, Dombeya rotundifolia* and *Acacia caffra*) and shrubs, grasses and forbs associated with trees, from the species of the open areas. The first axis is therefore from cover to open, corresponding to the first axes of the *Acacia* transects, but is much more obscured in ordination variants by the irregular occurrence of species. Fewer species are closely associated with the trees and covered areas than with the openings. Centroids of all tree species are on the right end of axis 1 (Fig. 7), but almost all species have wide distributions along the axis (Table 7).

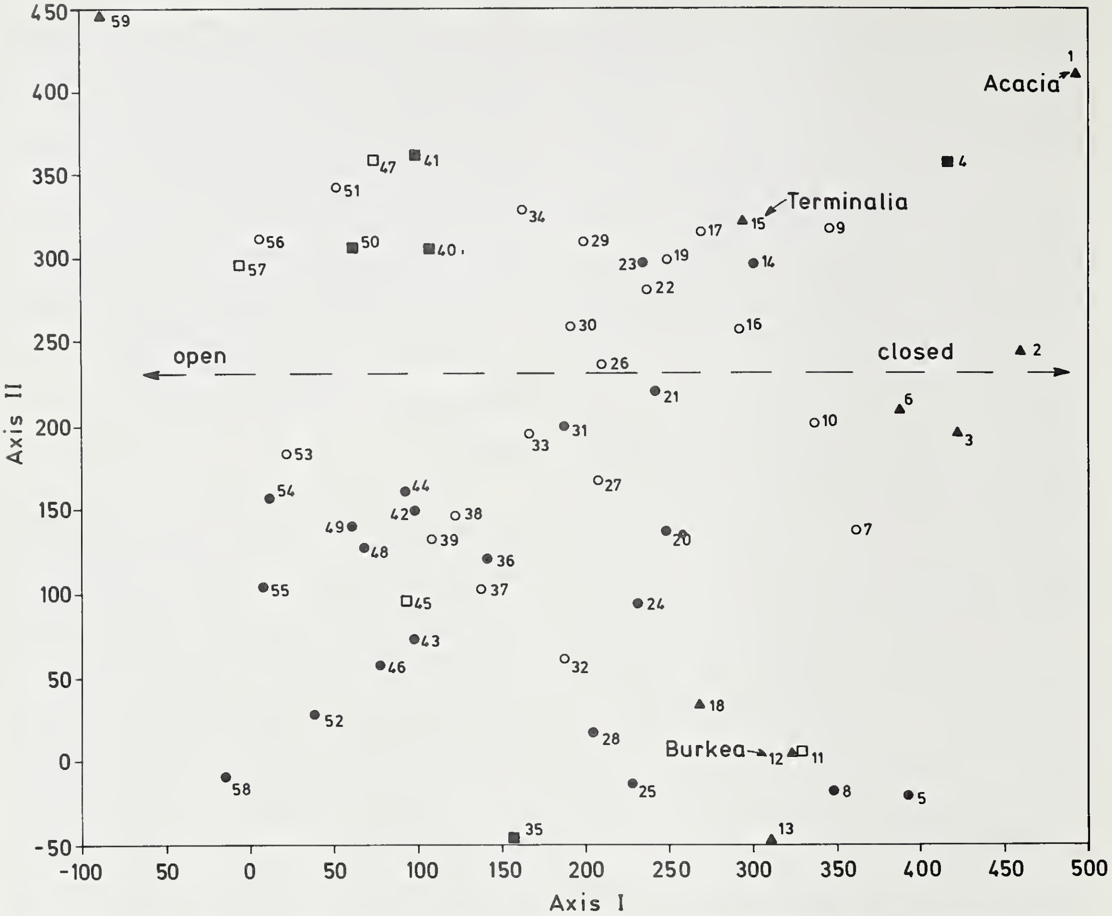

FIG. 7. — Ordination by DCA of 59 species in transect 1, open, recently burned *Burkea africana–Terminalia sericea* savanna. Numbers for species are given in Table 7; symbols for growth-forms are given in the legend for Fig. 2. The first axis extends from open quadrats, and species centered in these, to those with tree cover; the second axis reflects soil nutrient levels and the effects of the dominant species labeled.

The DCA profile for first-axis quadrat scores along the transect is given in Fig. 8. Scores above about 200 correspond in general to the covered patches, and the highest scores correspond to cover of two less common tree species — *Acacia caffra* and *Dombeya rotundifolia.* The grass *Panicum maximum* again is clearly associated with tree cover; other understory species largely associated with the trees include the grass *Schizachyrium jeffreysii*, the shrubs *Protasparagus suaveolens* and *Grewia flavescens*, and the forbs *Pollichia campestris, Hibiscus pusillus* and *Tragia rupestris*. It is difficult in this vegetation, in which some tree patches are rather open and diffuse, and others are individual trees with limited effect on undergrowth, to recognize any quality of boundedness in the pattern (cf. Whittaker *et al.*, 1979a,b, and transect 3, above).

The second axis of Fig. 7 separates quadrats containing *Terminalia sericea* (or *Acacia caffra*) from *Burkea africana* and the other tree species, and it also divides quadrats from the open areas into two arms (connected by intermediate quadrats and species) extending from a central core toward the upper and lower left corners of the diagram. Of the 10 ordinations of 100-m segments of the transect, six gave first axes also representing open-to-cover gradients; three of the other four gave *Burkea*-to-*Terminalia* first axes. In five of the 10 ordinations the first and second axes together included the open-cover and *Burkea–Terminalia* gradients; in other cases both axes represented one of these gradients, or one axis was uninterpretable.

The second axes of all these ordinations are strongly affected by broad species occurrences and irregular behaviour, but the *Burkea–Terminalia* axis is interpreted as primarily one of nutrient relationships. Although there are marked deviations, the trace of DCA axis 2 values (Fig. 8B) tends to start at high values (between 186 and 278 at the beginning of the transect) and to drop gradually to lower values (between 93 and 186 at the end of the transect). Calcium concentrations in soil samples taken along the transect at 50-m intervals, superimposed on the trace of axis 2 (Fig. 8B), show generally decreasing concentrations from the start to the end of the transect. (The Ca concentration at 325 m corresponds to a peak on the axis 1 trace and to a patch of *Acacia caffra*. In Table 8b, values for soil Ca and other nutrients are given, with samples divided into sets

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with high, mid-range and low scores for the second axis of DCA ordination). With some exceptions, samples in the high score group are at the beginning or toward the middle of the transect, whereas the samples in the low score group are located toward the end (top) of the transect. Mean values for three cations, Ca, K and Mg, decrease with decreasing DCA score and along the transect. Although the terrain is almost level, the transect extended up a gentle slope from its beginning, near an open valley, to its end. Slight soil differences, representing a fraction of a catena, are therefore to be expected and may be identified in the results given in Table 8a.

For the covered half of the ordination the nutrient relations of axis 2 involve additional effects, those of dominant tree species. As these effects were suspected from preliminary interpretation of the ordination, additional soil samples were collected and analysed from specific sites — under canopies of *Burkea* and *Terminalia* at the beginning (75 m) and end (1 025 m) of the transect and from under *Acacia caffra* at 325 m with 'control' samples from open areas corresponding with each under-tree site. Results are given in Table 8b. Al and Fe are concentrated in the soil beneath *Burkea* relative to both open sites and the other tree species, whereas Mn is particularly low under *Burkea*. In contrast, Ca, K, and Mg are concentrated under *Terminalia* and *Acacia* relative to *Burkea* and (less clearly) relative to open sites. The subhabitats with legumes, namely under *Burkea* and *A. caffra*, had approximately double the NO_3-nitrogen concentration of the other soils; *Burkea* and all the *Acacia* species at Nylsvley produce nodules and are probably fixing N (Grobbelaar *et al.*, 1967; Grobbelaar & Clarke, 1975). Zn and P are at very low concentrations in all subhabitats.

From the upper to the lower end of the transect there is (a) some increase in mean soil nutrient levels, (b) a (scarcely significant) increase in the fraction of fine particles in the soil, (c) some shift in the relative importance of *Burkea africana* and *Ochna pulchra* vs *Terminalia sericea* in the tree stratum (Table 3), although these and other major species occur through the length of the transect, and (d) some shift in the relative numbers of quadrats having low, vs high, scores on the second axis of the ordination. We therefore judge that there is a subtle macrogradient in soil nutrient levels along the transect, but also subtle microgradients in soil nutrient levels within segments of the transect as affected by openings and tree species. The nutrient relations are complex, but the ordination suggests that many species are responding similarly to the macro- and microgradients. Their responses to the latter represent the primary meaning of the second axis of the within-community pattern in this woodland. The full meaning of the species responses to cover of *Burkea* vs *Terminalia* within segments of the transect cannot yet be established; but we suspect that *Burkea* may be somewhat better adapted to sterile soils, and *Terminalia* somewhat better at accumulating or pumping major nutrients (excepting N) from the soil into the litter and upper soil layers in which subordinate plants are rooted. In a continuing study, we are investigating nutrient concentrations in the foliage of and litter beneath tree species and measuring plant growth response and nutrient uptake on the different subhabitat soils (e.g. Olsvig-Whittaker & Morris, 1982).

The relationship of the open quadrats to the second axis is less clear. Field observation suggests, however, that the species in the lower left quadrant of Fig. 7,

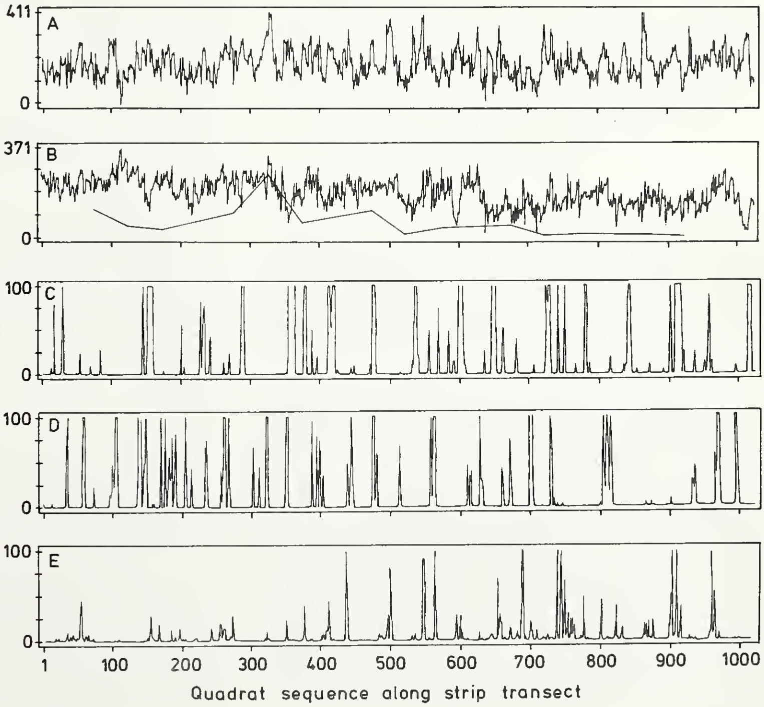

FIG. 8. — Traces of ordination and tree-species scores along the field sequence of 1 025, 1-m² quadrats of transect 1, open *Burkea africana* savanna-woodland: A, quadrat scores on the first DCA axis, from low scores for open to high for covered quadrats; B, quadrat scores on the second DCA axis, from low scores for lower to high scores for higher soil nutrient concentrations and a superimposed trace of Ca concentration (ppm) from soil samples taken at 50-m intervals; C, cover per cents for *Burkea africana*; D, cover per cents for *Terminalia sericea*; E, cover per cents for *Ochna pulchra*. The ordinate scales are in SD units (X 100) for the upper two panels, per cents of cover for the lower three panels.

TABLE 8a. — Results, means, and standard deviations of soil texture analyses of samples from 50 m intervals along transect 1, sequenced by mean axis 2 DCA quadrat score for sample quadrat on either side for (a) high mean DCA score, (b) mid-range, and (c) low mean score

Quadrat number	Mean DCA score (axis 2)	[a]Sand	Silt	Clay	Sand/Clay	Sand/Silt
(a)						
125	291	90.7	4.1	5.2	17.4	22.1
75	285	84.6	9.1	6.3	13.4	9.3
275	242	90.6	4.7	4.7	19.3	19.3
175	240	91.0	3.9	5.1	17.8	23.3
975	219	86.6	7.1	6.3	13.7	12.2
625	217	91.8	4.4	3.8	24.2	20.9
575	210	93.5	1.9	4.6	20.3	49.2
325	189	89.1	5.5	5.4	16.5	16.2
Mean		89.7	5.1	5.2	17.8	21.6
s.d.		2.9	2.2	0.9	3.5	12.2
(b)						
875	182	89.6	4.2	6.2	14.5	21.3
425	179	91.3	3.2	5.5	16.6	28.5
225	176	91.9	2.9	5.2	17.7	31.7
475	172	92.7	2.8	4.5	20.6	33.1
Mean		91.4	3.3	5.4	17.4	28.7
s.d.		1.3	0.6	0.7	2.5	5.3
(c)						
825	159	89.0	3.8	7.2	12.4	23.4
375	156	91.7	3.4	4.9	18.7	27.0
1025	144					
675	130	92.6	4.0	3.4	27.2	23.2
525	122	92.5	2.3	5.2	17.8	40.2
925	119	91.7	3.6	4.7	19.5	25.5
775	113	92.0	1.4	6.6	13.9	65.7
725	104	91.1	3.2	5.7	16.0	28.5
Mean		91.5	3.1	5.4	17.9	33.4
s.d.		1.2	0.9	1.3	4.8	15.4

[a] US standard particle sizes: sand 2.0–0.5 mm
silt 0.5–0.002 mm
clay <0.002 mm

many of which are graminoids, are characteristic of sandier and more strongly leached soils, those of the upper left quadrant, many of which are forbs, are characteristic of less sandy, less strongly leached, and sometimes moister soils.

We judge that the woodland studied with transect 1 is significantly patterned, with one major axis of species and quadrat differentiation related primarily to cover, and the other to soil fertility. The axes were difficult to recognize because the community is (a) rich in species with, probably, a number of species of similar adaptation able to replace one another in a given quadrat, (b) irregular in its pattern both because of this richness and because of the effects of frequent fire, and of animals, in reducing cover and permitting establishment of seedlings outside their optimum ranges in the pattern, while (c) the degree of the pattern differentiation (pattern diversity, as discussed above) is not great; many species can occur along much or all of the ranges of environmental conditions represented by the ordination axes. Matrix randomization tests suggest that, despite the stochastic quality of the data, the first two ordination axes express significant order in the data and the third axis probably does so, whereas the fourth eigenvalue is not significantly different from those for randomized data.

Higher axes of the ordinations gave high eigenvalues and SD values (EV = 0.341 and 0.304, SD = 4.01 and 3.31 for the third and fourth axes of the DCA). No correlations with environment were established for these axes, and their extremes were dominated by uncommon or rare species. These axes and the randomization experiments show that ordinations, given extensive and noisy data, can arrange uncommon and chance combinations of species toward the ends of axes in ways that yield high SD lengths and eigenvalues for which the uncommon species are largely responsible. For transect 1 we further suspect, but cannot demonstrate, that many occurrences of uncommon species are not simply chance, but are made possible by local effects of animals that are not known to us and could not be interpreted except by detailed observations on such effects. The apparent degree of randomness of species distributions along the transect and in relation to all ordination axes may be consequent on local animal disturbances and fertilization that are an important part of the pattern but that we cannot treat systematically.

Other pattern measurements

Given the large number of samples — 1 025 quadrats — the adjoining pairs test gave very high improbabilities of random distribution for almost all species. Probabilities of randomness were less than 0.000001 for all the major graminoid species and for the three dominant trees. Of 83 species with more than 20 occurrences in the transect, the only species not significantly different from randomness by the test were *Ledebouria* sp. (94 occurrences) and *Euphorbia trichadenia* (56). Despite the high probabilities of contagion, the tests for scale of contagion were uniformly negative (with monotonic trends in $\sigma^2/\bar{x}$, $(\sigma^2 - \bar{x})/\bar{x}$, and χ^2) or weak and doubtfully significant. No scale of contagion was indicated for *Burkea africana*; scales were weakly suggested at 9 m for *Ochna pulchra* and 15–16 m for *Terminalia sericea*. For a few other species scales ranging from 7–8 m to 16–18 m were suggested; but the indications appear in only one of the several tests and are probably nonsignificant. The tests for periodicity give a very weak suggestion of period at 32–33 m (mean DCA score difference of 0.717 for this distance, vs a background difference of 0.773 for other distances). Measures of species association gave high probabilities of association for many pairs of species, but it was not found possible to relate these species into groups associated with each other and distinct from other groups of associates. Numerical classification by Twinspan provides a different approach to recognition of groups of associates. Results were generally negative in the sense that noda of Twinspan were defined primarily by single major species, not by groups of associated indicator species. The results of these supplementary tests are consistent with the ordinations in suggesting a pattern that is strongly patchy but

TABLE 8b. — Results, means, and standard deviations of chemical analyses of soil samples from 50 m intervals along transect 1, sequenced by mean axis 2 DCA quadrat score for sample quadrat and quadrat on either side for (a) high mean DCA score, (b) mid-range, and (c) low mean score

Set numbers	Quadrat number	Mean DCA score (axis 2)	pH	Ex H me/100 g	ppm					
					P	K	Mg	Ca	NO_3 N	NH_4 N
(a)										
299/14	125	291	5.1	2	0.5	48	38	95	2.5	2.0
362/27 & 299/13	[a]75	285	5.0	4	0.5	38	55	173	[b]<2.5	2.5
299/1	275	242	5.3	4	1.0	45	50	163	2.5	3.0
299/15	175	240	5.0	2	0.5	35	33	75	[b]<2.5	2.5
299/12	975	219	5.1	3	0.5	28	50	120	2.5	1.5
362/24	625	217	5.4	2	0.5	45	48	213	[b]<2.5	2.5
299/6	575	210	4.8	2	0.5	25	25	85	2.5	2.0
299/2	325	189	5.7	4	1.0	105	108	450	2.5	3.0
	Mean		5.2	2.9	0.6	46.1	50.9	[c]171.8	2.3	2.4
	s.d.		0.28	0.99	0.23	25.20	25.20	122.28	0.26	0.52
(b)										
299/10	875	182	4.7	3	0.5	30	13	45	2.5	2.0
362/26	425	179	4.6	2	0.5	40	25	80	8.0	8.0
362/23 & 29	225	176	4.7	2	0.5	28	23	58	[b]<2.5	2.5
299/4	475	172	5.3	4	1.0	63	73	175	2.5	2.5
	Mean		4.8	2.8	0.6	40.3	33.5	89.5	3.8	3.8
	s.d.		0.32	0.96	0.25	16.05	26.85	58.80	2.84	2.84
(c)										
362/25	825	159	4.6	3	0.5	30	18	50	[b]<2.5	2.5
299/3	375	156	4.9	4	1.0	50	40	105	5.0	3.0
362/28	1025	144	4.4	3	0.5	20	10	45	2.5	3.0
299/7	675	130	5.3	3	0.5	48	40	90	2.5	2.0
299/5	525	122	4.8	2	0.5	35	18	50	2.5	2.0
299/11	925	119	4.5	3	1.0	28	10	40	2.5	2.0
299/9	775	113	4.6	4	0.5	35	18	50	2.5	2.5
362/22 & 299/8	725	104	4.6	3	0.5	59	20	45	5.0	4.0
	Mean		4.7	3.1	0.6	38.1	21.8	59.4	3.1	2.6
	s.d.		0.29	0.64	0.23	13.04	11.88	24.12	1.21	0.69

[a] Where two sets contribute, value given is mean
[b] Taken as 2.0 in calculations of mean and s.d.
[c] Omitting quadrat 325 $\bar{x} = 132.0$, s.d. = 51.92

weakly ordered, marked by conspicuous contagion but with relatively uncoordinated and irregular occurrence of species in the pattern. Such co-ordination of species occurrences as exists — in relation to cover and nutrient levels — could be recognized through ordination but not with these other techniques.

Spectral analysis

Using the upper 650 m of the transect, correlograms and power spectra were examined for 18 species selected both for abundance (as excessive zeros interfere with the analysis) and because of indications of the species' roles in the DCA ordinations. The dominants, in terms of variance in their log transformed cover, were the three trees, *Burkea, Terminalia* and *Ochna*, with the respective variances 2.78, 2.09, and 1.55. Of all the species examined only *Burkea* showed sufficiently distinct periodicity for a clear secondary peak in its correlogram (Fig. 9). This peak was centered at 60 m, and the power spectrum correspondingly peaked at a wavelength of 60 m. Since *Burkea* was also the species with the greatest variance, it was reasonable to search first for a community pattern organized around its periodicity at 60 m.

Of the other trees, *Ochna* did concur with *Burkea* in showing its power spectral peak at a wavelength of 60 m, but *Terminalia* peaked instead at 36 m. Inspection of the correlogram for *Terminalia* shows a shallow secondary peak at 32 m and another at 71 m. The longer wavelength peak, which may be the analog of the 60 m pattern in *Burkea africana*, is actually a slightly stronger positive serial correlation, but the two are near enough in phase that the spectral analysis combines the two into a single spectral peak. Incidentally, this example illustrates how a weak correlogram may transform into a distinct power spectrum. The serial correlations in the secondary peaks and minima for *Ochna* are all quite

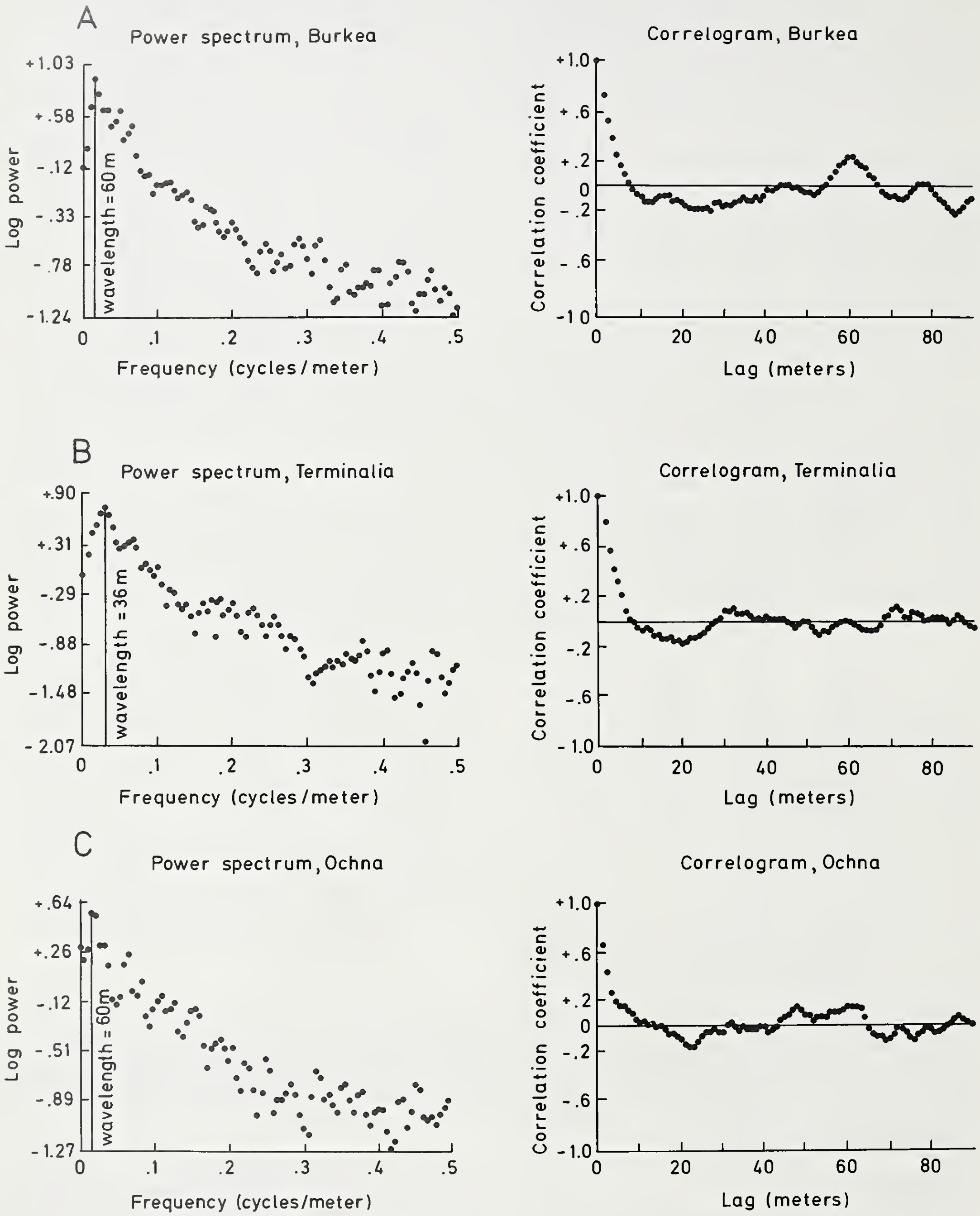

FIG. 9. —Power spectra (left) and correlograms (right) for the three major tree species, transect 1. A, *Burkea africana*; B, *Terminalia sericea*; C, *Ochna pulchra*.

small in magnitude, yet they are aligned in such a way as to indicate the presence of a definite and persistent periodic signal, albeit amongst much noise.

The 60 m wavelength was not much in evidence in the spectra of other species, appearing clearly only in the herb *Cleome maculata*. Spectral peaks at 36 m or 30 m — adjacent wavelength intervals at the resolution of our calculations — were prominent in the grasses, *Elionurus muticus* and *Eragrostis pallens*, and the forbs *Pentarrhinum insipidum* and *Evolvulus alsinoides*.

Exploratory cross spectra were computed for all species crossed with *Burkea* and all species crossed with *Eragrostis pallens*. Most of the cross spectra showed a local peak in coherence at the 60 m wavelength or the 30 m one (some at 36 m) and some showed both. The consistency of this evidence of pattern repeating every 30 m and/or every 60 m prompted the selection of the corresponding frequencies, 0.03333 m^{-1} and 0.01667 m^{-1}, for the frequency domain principal components analysis (PCA).

The cross spectrum matrix at frequency 0.01667 m^{-1} was obtained from the fourth cross spectral element when the autocovariance and crosscovariance calculations were carried out for 90 lags at intervals of 1 m. When the eigenanalysis was performed directly on this matrix, the first resultant eigenvector accounted for 67% of the variance at this frequency, with 18% accounted for by the next largest eigenvector. The first eigenvector was dominated entirely by the three tree species, as a consequence both of their greater overall variance and of their more distinct spectral peaks at this particular frequency (Fig. 10A). The greatest contribution was made by *Burkea*, with the next greatest contribution coming from *Terminalia*, the latter being exactly out of phase with the former. *Ochna* did not participate as strongly in the pattern, and its contribution was in an intermediate phase position between the other two. The second eigenvector (Fig. 10B) was dominated by *Ochna* with the only other distinct contribution coming from *Terminalia*, again at 90° out of phase with *Ochna*, but in the opposite direction (leading as opposed to lagging) from the relationship between the two in eigenvector 1. This suggests a wave structure based on individuals of *Burkea* occurring every 60 m, with individuals of *Terminalia* tending to occur (though not quite so regularly) equispaced between them. The position of *Ochna* was less regular still, tending most often to occur to one side of the *Terminalia*, between it and the *Burkea*, though at other times occurring to the other side of *Terminalia*, and without regard for the pattern of *Burkea*. The other species did not contribute detectably to this pattern.

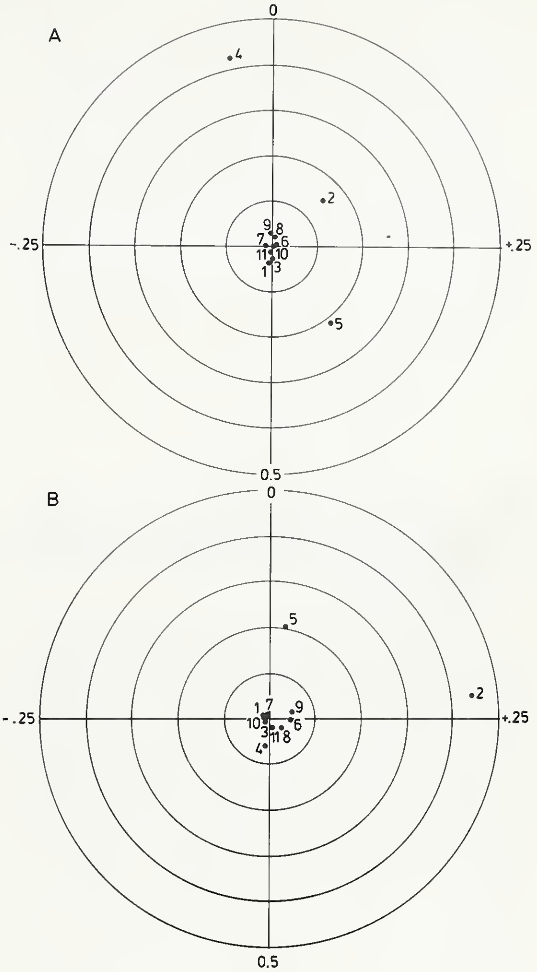

FIG. 10. —Frequency domain PCA for 11 species of transect 1 for a 60-m wavelength, using cover values for species: A, first eigenvector; B, second eigenvector. Plot is in polar coordinates, where radius represents intensity of that species contribution to the pattern, and angle represents its relative position (phase) in the wave structure. The high variances of the three tree species dominate the analysis. Results suggest a wave structure of tree clumps every 30 m, with *Burkea* and *Terminalia* fully out of phase and alternating in these clumps (first eigenvector), whereas *Ochna* occurs more irregularly, 90° out of phase with *Terminalia*. Species numbers for Figs 10–12: 1 = *Justicia anagalloides*; 2 = *Ochna pulchra*; 3 = *Elionurus muticus*; 4 = *Burkea africana*; 5 = *Terminalia sericea*, 6 = *Diheteropogon amplectens*; 7 = *Cassia mimosoides*; 8 = *Aristida stipitata*; 9 = *Fadogia monticola*; 10 = *Pentarrhinum insipidum*; 11 = *Parinari capensis*.

In an effort to prevent variances of the three tree species from overwhelming the pattern, the sequence of log transformed cover observations of each species was standardized to unit variance. This still permitted the species to differ with respect to the amount of variance at the chosen frequency. The eigenanalysis of the matrix of cross spectra at 0.01667 m^{-1} showed 38% of the variance now accounted for in the first eigenvector, and 19% in the second eigenvector. The positions of the three tree species remain much the same in the wave structure depicted by the first eigenvector (Fig. 11). *Burkea* dominates the pattern, *Terminalia* is exactly out of phase with it, and *Ochna* is 90° out of phase with both, leading one and lagging the other. Now, however, we also see a contribution from other species to the pattern. *Justicia anagalloides, Pentarrhinum insipidum,* and *Elionurus muticus* are associated with the *Terminalia* phase; *Fadogia monticola* is associated with the *Burkea* phase; and *Cassia mimosoides* and *Aristida stipitata* are each 90° out of phase with these, and respectively out of phase and in phase with *Ochna*.

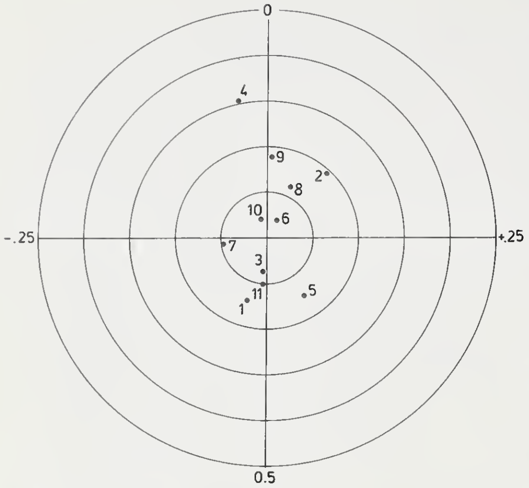

FIG. 11. —Frequency domain PCA for 11 species of transect 1 for 60-m wavelength with data standardized. Log-transformed cover values have been standardized to unit variance to avoid variance-dominance by the trees. For key to species numbers see legend of Fig. 10.

It seemed a little strange that the preponderance of the phases depicted in this wave structure included trees. The only distinct contribution that was not in phase with one of the trees was that of *Cassia mimosoides.* Three plausible hypotheses suggest themselves. The most direct interpretation, though biologically the least plausible, is that this is indeed the way the vegetation is organized: the various tree species define specific and regularly spaced patches, and the other species contributing to the pattern are each associated with one tree or another, with only *Cassia mimosoides* defining a non-tree type of patch. A second interpretation, which illustrates one of the possible ways in which spectral analysis may pound square pegs in sinusoidal holes, is that the non-tree species which appeared in this pattern occurred primarily in some distinct clumps which chanced to be located where one or the other of the trees 'should have been', in the sense that this patch was 60 m from one of the trees, and that the repeating pattern of trees at 60-m intervals was not perfect but had some trees 'missing'. Then a particular species might appear in a tree phase without actually occurring in the same patch with that tree. The third interpretation is that even though the 60 m wavelength was the correct scale at which to examine the interrelationships between the trees, it is not appropriate for an examination of the relationships between trees and non-tree vegetation, because the non-tree vegetation is organized in a pattern which simply is inserted between trees, regardless of tree species, and therefore should be sought at the finer scale at which trees (of any sort) are absent rather than the long scale at which trees of a particular species are present.

A composite variable formed by adding up the total tree cover in each quadrat revealed a peak in its power spectrum at the frequency 0.03333 m^{-1}. This indicated that the third hypothesis was quite likely, though of course it did not rule out the other two. Composite variables formed of grasses also showed a power spectral peak at the 30 m wavelength, as did some of the individual species referred to earlier. Accordingly, the frequency domain PCA was repeated by selecting the fourth cross spectral element from calculations carried out for 45 lags, for a cross spectrum matrix at the frequency 0.03333 m^{-1}.

Eigenanalysis of the matrix of cross spectra at this frequency showed the pattern still to be dominated by the three trees, owing again to their overwhelming variance. Standardizing the species log cover values to unit variance removed this problem, but eigenanalysis of the resulting matrix of cross spectra did not resolve sufficiently distinct eigenvectors. The first eigenvector accounted for 27% of the variance at this frequency and the second accounted for 21%. A different normalization was attempted by dividing each off-diagonal element a_{ij} of the matrix of cross spectra by the geometric mean of the corresponding diagonal elements a_{ii} and a_{jj}, and then replacing the diagonal with ones. This standardized the power of each species to unity, so that each species displayed the same amount of variance at the particular frequency being examined. Under this normalization the separation between the first two eigenvectors was more satisfactory. The first eigenvector accounted for 26% of the variance in the normalized system at this frequency, and the second accounted for 17%.

The first eigenvector in the 30 m pattern pulled together the three tree species to very similar phase angles (Fig. 12). *Burkea* and *Terminalia* are almost exactly in phase and *Ochna* is off by about one-eighth of a cycle. This 30 m wavelength pattern thus revealed a 'tree phase' which was not seen in the 60 m pattern. This does not indicate that all three tree species co-

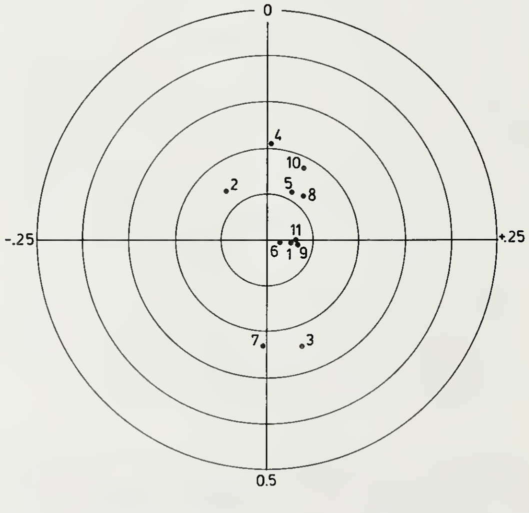

FIG. 12. —Frequency domain PCA for 11 species of transect 1 with a standardization equalizing the variances of species, using a 30-m wavelength. With this treatment the three tree species, *Burkea, Terminalia* and *Ochna* (4, 5, 2), are grouped as a tree phase, whereas *Cassia mimosoides* (7) and *Elionurus muticus* (3) are fully out of phase with these and represent openings alternating with the tree clumps. For key to species numbers see legend of Fig. 10.

occurred in patches that were spaced at about 30-m intervals (indeed they did not). Rather it shows that trees of one sort or another were to be encountered about every 30 m, and the 60 m analysis indicates that the actual species pattern was essentially a checkerboard of *Burkea* alternating with *Terminalia*, whereas *Ochna* was scattered less regularly, sometimes replacing or accompanying one species and sometimes the other. We find in Fig. 12 that two species, *Cassia mimosoides* and *Elionurus muticus*, now alternate with the tree phase. These then are the species most typical of the centers of the openings between trees. *Pentarrhinum insipidum* and *Aristida stipitata* remain associated with the tree phase.

The number of species participating strongly in the spatial patterning remained small, even in the 30 m wavelength analysis. Some species, most notably *Eragrostis pallens*, had shown a local peak in their power spectra at a frequency of 0.1000 m^{-1}. On the chance that this shorter wavelength might correspond to a scale at which the grasses and herbs might be organized in a repeated pattern, we investigated the associated cross-spectral matrix at this frequency. The trees continued to dominate the pattern, and when these three species were removed the frequency domain PCA failed to resolve distinct axes, except for a clear relationship between *Eragrostis pallens* and *Elionurus muticus* revealed when no normalization was done (Fig. 13). These two species tended to form a wave structure in which they were 90° out of phase but with no consistency as to which was leading and which was lagging, suggestive of a tendency to form adjacent patches of just a few m extent.

The vegetation pattern of transect 1 is unusually complex. The number of species is large, and most of these occurred in patches that were too widely dispersed for a repeating pattern of distribution to be detected. Further, the dominant phase of the vegetation, the trees, did not occur as patches of uniform composition but rather as three distinct species that did not intermingle on a scale commensurate with the major periodicities in the vegetation. Most of the other species occurred too infrequently to show any pattern except for their response to the presence or absence of trees.

Given the complexity of the vegetation, the spectral analysis did not perform badly. We succeeded in identifying two major wavelengths on which the community pattern was organized, and we were able to attach reasonable biological interpretations to the analysis. Spectral analysis, and frequency domain PCA, demonstrated their strengths in responding sensitively to a pattern that involved organization at a considerable distance; and at the same time illustrated some of the interpretational ambiguities which may accompany this sensitivity.

Other transects in *Burkea* savannas

Ordination

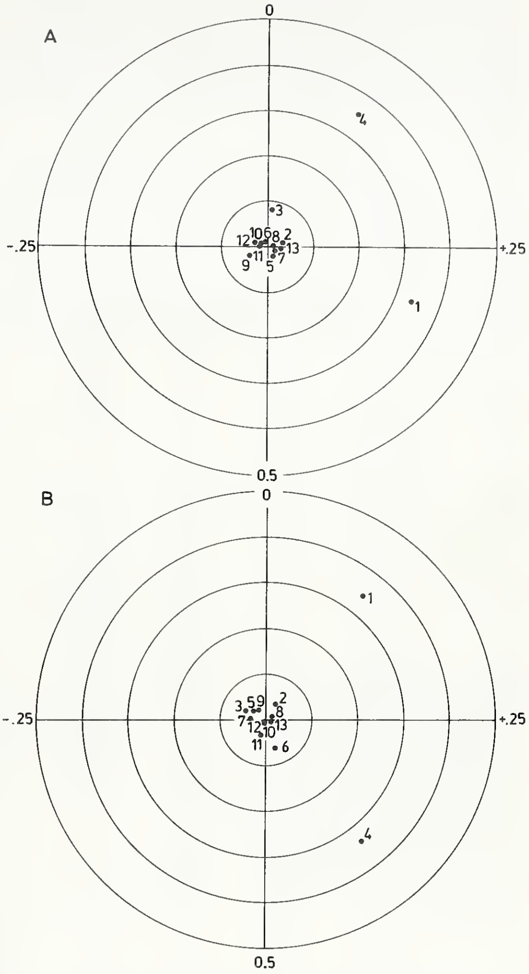

FIG. 13. — Frequency domain PCA for 13 understorey species of transect 1 without species standardization, using a 10-m wavelength: A, first eigenvector; B, second eigenvector. With the three tree species removed, *Eragrostis pallens* (1) and *Elionurus muticus* (4) dominate the analysis, 90° out of phase with each other in both eigenvectors. Other species are *Cleome maculata* (2), *Justicia anagalloides* (3), *Cyperus margaritaceus* (5), *Fimbristylis hispidula* (6), *Diheteropogon amplectens* (7), *Cassia mimosoides* (8), *Vernonia oligocephala* (9), *Aristida stipitata* (10), *Solanum panduriforme* (11), *Pentarrhinum insipidum* (12) and *Evolvulus alsinoides* (13).

Two shorter transects were taken from other phases of *Burkea* savanna in the hope that these and the long transect might complement one another. Transect 2 was close by and in much the same community as transect 1, but across a small road from it in a stand that had not been burned for at least 4 years. Transect 2 extended from this unburned *Burkea* savanna (transect 2a, 200 m) into a patch of *Acacia* savanna (transect 2b, 125 m), described in an earlier section. Transect 6 (200 m) was in a denser phase of *Burkea* woodland with higher tree cover and basal area (Tables 2 and 3) and less distinct openings. For both transect 2a and 6 the matrix randomization tests support the significance of the first two, but not of higher, ordination axes.

The DCA ordination of the full 325 quadrats of transect 2 divided it neatly into the *Burkea* and *Acacia* savannas on the first axis (EV = 0.718). The last part of the 200-m strip in *Burkea* savanna (transect 2a) was shown by the ordinations to be distinct from the remainder and some species were concentrated in this transition from *Burkea* to *Acacia* savanna (*Tristachya rehmannii, Trachypogon spicatus, Rhynchelytrum setifolium, Parinari capensis*).

The separate DCA analyses of the *Burkea* section, transect 2a, gave a clear gradient on the first axis from closed *Burkea*- and *Ochna*-dominated quadrats to quadrats of the intervening open areas. Species distributions on the first two axes (EV = 0.570, 0.426), for an ordination scaled by species maxima and omitting species in fewer than five quadrats, are shown in Fig. 14. The trees *Ochna pulchra, Burkea africana*, and *Dombeya rotundifolia* as well as the shrub *Grewia flavescens* are at the right hand of axis 1, with the trees *Terminalia sericea* and *Combretum zeyheri* near the center of the axes. Species associated with *Burkea, Ochna*, and the covered end of the axis include the grass *Panicum maximum* and the forbs *Pollichia campestris, Solanum panduriforme, Senecio inaequidens, Commelina erecta*, and *Pentarrhinum insipidum* (Table 9).

Species at the open end of the first axis, including many grasses, are divided by the second axis into two arms originating in a central core. Species of open areas loosely associated with *Terminalia* and *Combretum zeyheri* clumps include the graminoids *Eragrostis pallens* and *Elionurus muticus* (which are widespread in the transect) and other species in the upper left quadrant of Fig. 14. Species at the other end of axis 2, in the lower left quadrant of Fig. 14, include several less frequent graminoids and forbs, the geoxylic suffrutices *Parinari capensis* and *Elephantorrhiza elephantina* and the shrub *Lannea edulis*. No geoxylic suffrutices are associated with the preceding group. As in the other transects, a number of species with wide occurrence are located in the center of the ordination figures; for transect 2b these matrix species include a number of graminoids and the three annual forbs of the genus *Justicia* (Table 9).

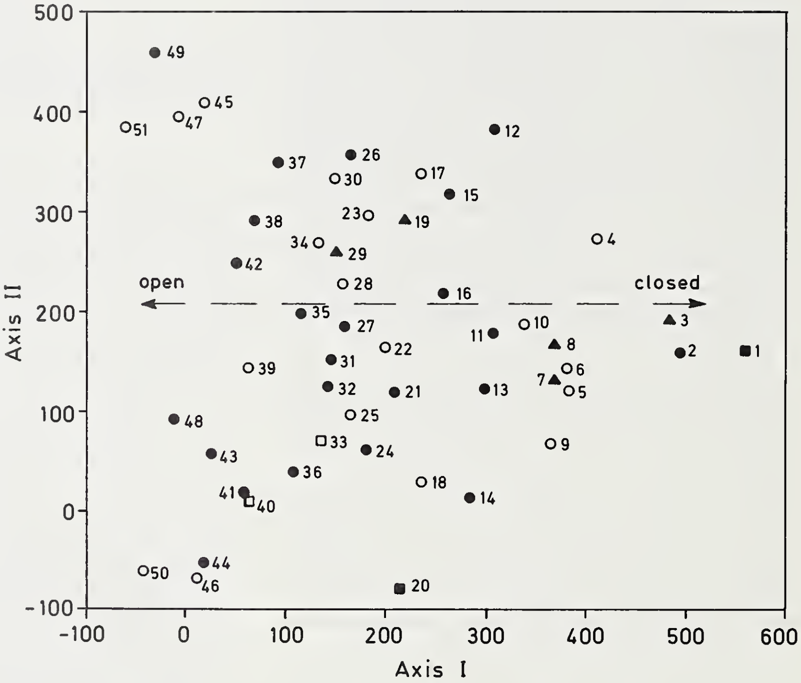

FIG. 14. Ordination by DCA of 51 species of transect 2a, a *Burkea africana* savanna not burned for at least 4 years. Species numbers are given in Table 9. Quadrats with tree cover and species centered in them are ordinated toward the right on axis 1; different phases of the openings, left on axis 1, are distinguished on axis 2.

The first axis of the ordination of transect 2a shows fairly good agreement with the first axis of transect 1, the principal transect; but the second axes do not correspond. Species identified as low in nutrient status in transect 1 occur in the central core and both left-hand arms of transect 2a; higher nutrient status species are similarly dispersed in the ordination field and mixed in position with those of lower nutrient status. The differences between the two ordinations seem not simply the consequence of fire. Despite the effort to place the two transects in stands alike in all respects but time of fire, the differences may result from unrecognized soil differences related to the close proximity of transect 2a to *Acacia* savanna.

TABLE 9. — Species characterization and distribution in a DCA ordination of transect 2a, unburned open *Burkea africana* savanna

Species	Transect ranges										Score on DCA axis 1 (× 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
	1 closed	2	3	4	5	6	7	8	9	10 open						
1. *Grewia flavescens*	[a]+	+	+	+	+	–	+	–	+	–	556	0.5	[b]14	Sbd	Pn	2.00
2. *Panicum maximum*	+	+	–	+	–	–	–	–	–	–	493	0.2	12	Hgp	Hsc	0.40/0.8
3. *Dombeya rotundifolia*	2	+	–	–	–	–	–	+	+	–	483	2.1	10	Tbd	Pmi	2.50
4. *Pollichia campestris*	+	+	–	+	+	+	–	–	–	–	410	0.1	10	Hpd	Hsc	0.40
5. *Commelina erecta*	+	+	+	+	+	+	+	–	–	–	384	0.1	28	Hpd	Hsc	0.15
6. *Senecio inaequidens*	+	+	+	+	–	+	+	+	+	–	380	0.1	15	Hpd	Hsc	0.60
7. *Burkea africana*	9	7	4	2	1	+	+	–	+	+	369	23.2	79	Tbd	Pmi	3.00
8. *Ochna pulchra*	2	1	+	+	+	+	+	+	+	+	368	4.6	85	Tbd	Pmi	2.50
9. *Pentarrhinum insipidum*	+	+	+	+	–	–	–	+	–	+	364	–	13	Has	Tsc	0.15
10. *Solanum panduriforme*	+	+	+	+	+	–	–	–	–	–	337	0.1	9	Hpd	Csf	0.30
11. *Rhynchelytrum setifolium*	+	+	+	+	+	+	+	–	–	–	306	0.3	11	Hgp	Hsc	0.25/0.6
12. *Schizachyrium sanguineum*	–	+	+	–	+	–	–	–	–	+	306	0.3	5	Hgp	Hsc	0.40/0.9
13. *Urelytrum squarrosum*	+	+	+	+	–	+	–	–	+	–	299	0.5	10	Hgp	Hsc	0.90/1.5
14. *Tristachya rehmannii*	+	1	+	+	+	+	+	+	+	+	281	3.3	43	Hgp	Hsc	1.50/2.0
15. *Rhynchelytrum repens*	+	–	+	+	–	+	–	–	–	–	261	–	5	Hga	Tsc	0.30/0.6
16. *Setaria perennis*	1	1	1	1	1	1	+	1	+	+	255	9.4	163	Hgp	Hsc	0.30/0.6
17. *Cyphocarpa angustifolia*	+	+	+	+	+	–	–	+	+	–	235	–	8	Has	Tsc	0.30
18. *Euphorbia trichadenia*	+	+	+	–	+	+	+	–	–	+	235	–	8	Has	Tsc	0.20
19. *Terminalia sericea*	+	+	+	1	1	+	+	–	+	+	216	5.7	40	Tbd	Pmi	3.00
20. *Lannea edulis*	–	+	+	–	+	–	–	–	+	–	212	0.1	5	Sbd	Pmi	2.50
21. *Themeda triandra*	+	+	+	+	+	+	+	+	+	+	206	0.7	50	Hgp	Hsc	0.60/1.0
22. *Talinum caffrum*	–	+	–	+	+	+	–	–	+	–	199	–	6	Has	Tsc	0.10
23. *Fadogia monticola*	+	+	+	+	+	+	+	+	+	+	183	1.0	48	Hpd	Hsc	0.50
24. *Perotis patens*	–	–	+	+	+	+	–	–	–	+	180	–	11	Hgas	Tsc	0.15/0.3
25. *Justicia minima*	+	+	+	+	+	+	+	+	+	+	164	1.5	156	Has	Tsc	0.20
26. *Aristida argentea*	–	+	–	–	–	+	–	–	+	–	164	–	5	Hgp	Hsc	0.20/0.6
27. *Brachiaria serrata*	+	+	+	+	+	+	+	+	+	+	158	0.3	37	Hgp	Hsc	0.20/0.5
28. *Justicia pallidior*	+	+	+	+	+	+	+	+	+	+	157	0.7	111	Has	Gs	0.20
29. *Combretum zeyheri*	–	+	+	+	+	+	+	–	–	+	149	0.2	7	Tbd	Pmi	3.00
30. *Oldenlandia herbacea*	–	+	+	+	+	+	+	+	+	+	147	0.1	24	Has	Tsc	0.40
31. *Aristida stipitata*	+	+	–	+	+	+	–	+	+	+	145	0.1	11	Hgp	Hsc	0.30/0.9
32. *Digitaria eriantha*	+	+	+	+	+	+	+	+	+	+	141	1.9	122	Hgp	Hsp	0.20/0.
33. *Elephantorrhiza elephantina*	–	+	+	+	+	+	+	+	+	+	135	0.2	38	Ssf	Cg	0.40
34. *Vernonia oligocephala*	–	+	+	+	+	+	+	+	+	+	131	0.2	33	Hpd	Hsc	0.50
35. *Diheteropogon amplectens*	+	+	+	+	+	+	+	+	+	+	115	1.3	91	Hgp	Hsc	0.80/1.2
36. *Aristida congesta* subsp. *congesta*	–	–	+	+	+	+	+	+	+	+	106	0.1	15	Hgp	Hsc	0.25/0.4
37. *Eragrostis pallens*	+	+	+	+	+	1	1	1	+	1	91	6.5	148	Hgp	Hsc	0.30/0.9
38. *Elionurus muticus*	+	+	+	+	+	+	+	+	+	+	69	3.5	110	Hgp	Hsc	0.30/0.6
39. *Justicia anagalloides*	–	+	+	+	+	+	+	+	+	+	61	0.2	47	Has	Tsc	0.20
40. *Parinari capensis*	–	+	+	+	+	+	+	+	+	+	57	0.4	30	Ssf	Cg	0.20
41. *Heteropogon contortus*	–	–	–	+	+	+	–	+	+	+	56	0.1	11	Hgp	Hsc	0.30/0.9
42. *Fimbristylis hispidula*	–	–	+	–	+	+	+	+	+	+	50	0.1	23	Hgp	Hsc	0.20/0.3
43. *Cymbopogon marginatus*	–	–	+	+	+	+	+	+	+	+	25	0.1	34	Hgp	Hsc	1.50/2.0
44. *Trachypogon spicatus*	–	–	–	+	–	+	+	+	+	+	19	0.2	9	Hgp	Hsc	0.25/1.0
45. *Waltheria indica*	–	–	–	+	–	+	+	–	+	+	17	0.1	11	Hpd	Hsc	0.50
46. *Cleome maculata*	–	–	–	–	–	+	+	+	+	+	12	–	10	Has	Tsc	0.50
47. *Evolvulus alsinoides*	–	–	–	–	–	+	–	+	+	+	-8	–	6	Has	Tsc	0.40
48. *Mariscus laxiflorus*	–	–	–	–	+	+	–	–	+	+	-13	–	8	Hgp	Hsc	0.30/0.5
49. *Schizachyrium jeffreysii*	–	+	–	–	–	+	–	–	+	+	-33	0.3	7	Hgp	Hsc	0.25/0.5
50. *Cyanotis speciosa*	–	–	–	–	–	–	–	–	+	+	-43	–	6	Has	Tsc	0.30
51. *Crabbea hirsuta*	–	–	–	–	–	–	–	–	+	+	-61	–	5	Has	Tsc	0.20
Mean number of species per quadrat in composite	7.7	8.7	9.1	10.5	10.2	10.6	9.4	8.1	11.4	10.0						

[a] Mean cover deciles in sets of 20 quadrats as ordinated.
[b] Number of occurrences in the strip of 200, 1-m² quadrats.

Transect 6 included many of the species of transects 1 and 2a, but also included some species absent from these, notably *Becium angustifolium* and *Hemizygia canescens* (Table 10). As in the other non-*Acacia* transects, species positions are variable in the variant ordinations; but the variations seem to relate to the overall triangular form illustrated in the ordination on the first two axes (EV's 0.569, 0.374; Fig. 15). The species groups suggested in this triangle are:

1. *Burkea africana*, with *Brachiaria serrata, Aristida argentea, Eragrostis lehmanniana, Cyperus margaritaceus, Perotis patens* and the geoxylic *Dichapetalum cymosum* as the extreme member of the group.

2. *Terminalia sericea* with *Becium angustifolium, Themeda triandra, Commelina africana* and *Waltheria indica.*

3. *Urelytrum squarrosum, Hemizygia canescens, Elephantorrhiza elephantina, Phyllanthus burchellii,* and *Eragrostis pallens*; these, and the upper right apex of the triangle, representing more open quadrats.

4. *Ochna pulchra* with *Justicia minima, Setaria perennis, Fimbristylis hispidula, Diheteropogon amplectens, Pollichia campestris* and *Digitaria eriantha* as a central matrix of companion species with wide distributions in the transect. The group may also include five species that are close to the *Burkea* group 1: *Commelina erecta, Mimusops* sp., *Mariscus laxiflorus, Oldenlandia herbacea* and *Elionurus muticus.*

These groupings reappear, with some shifting of species positions, in the ordinations without tree data. The groupings are not strongly related to those of transect 1. Associations of understory species with *Burkea* and *Terminalia* are different in transects 1 and 6, and the species of the open phase and matrix groups of transect 6 are recruited from species that are in widely different positions in the transect 1 ordinations, or are rare in or absent from that transect. Given the different soil and canopy pattern of transect 6, species may be responding in different ways from those in transect 1. Although the relationships to transects 1 and 2a are not strong, the ordination of transect 6 seems interpretable.

One major direction of pattern differentiation is from covered to open quadrats; this pattern gradient is angled toward the upper right of Fig. 15. A second major direction of differentiation, as in transect 1, is from *Burkea* and its associates to *Terminalia* and its associates; and this pattern gradient is angled from lower right to upper left in the ordination, Fig. 15. The pattern of transect 6 thus retains major features of the more open *Burkea* savanna of transect 1; but the extensive and differentiated open phase of the pattern of transect 1 is reduced to a single and more limited complex of quadrats and species in the denser vegetation of transect 6.

TABLE 10. — Species characterization in a DCA ordination of transect 6, denser *Burkea africana–Terminalia sericea* woodland

Species	Score on DCA axis 1 (X 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
1. *Urelytrum squarrosum*	384	1.5	[a]16	Hgp	Hsc	0.90/1.50
2. *Dichapetalum cymosum*	357	0.8	23	Ssf	Cg	0.10
3. *Burkea africana*	326	17.1	75	Tbd	Pmi	3.00
4. *Brachiaria serrata*	277	0.1	14	Hgp	Hsc	0.20/0.50
5. *Cyperus margaritaceus*	275		12	Hgp	Hsc	0.30/0.50
6. *Hemizygia canescens*	273	0.5	11	Hpd	Hsc	0.40
7. *Perotis patens*	270	0.2	38	Hgas	Tsc	0.15/0.30
8. *Aristida argentea*	265	0.5	33	Hgp	Hsc	0.20/0.60
9. *Panicum maximum*	259	0.5	27	Hgp	Hsc	0.40/0.80
10. *Eragrostis lehmanniana*	251	0.4	21	Hgp	Hsc	0.60/0.90
11. *Mimusops* sp.	231	0.5	16	Tbd	Pmi	2.00
12. *Elephantorrhiza elephantina*	228	0.5	52	Ssf	Cg	0.40
13. *Eragrostis pallens*	224	1.3	48	Hgp	Hsc	0.30/0.90
14. *Digitaria eriantha*	220	2.0	136	Hgp	Hsp	0.20/0.35
15. *Ochna pulchra*	190	19.3	157	Tbd	Pmi	2.50
16. *Justicia minima*	186	0.8	97	Has	Tsc	0.20
17. *Mariscus laxiflorus*	181	0.1	20	Hgp	Hsc	0.30/0.50
18. *Fimbristylis hispidula*	175	0.1	11	Hgp	Hsc	0.20/0.30
19. *Commelina erecta*	173	0.6	72	Has	Tsc	0.15
20. *Phyllanthus burchellii*	151	0.2	37	Has	Tsc	0.20
21. *Setaria perennis*	137	14.2	174	Hgp	Hsc	0.30/0.60
22. *Diheteropogon amplectens*	133	1.3	35	Hgp	Hsc	0.80/1.20
23. *Elionurus muticus*	125	0.3	15	Hgp	Hsc	0.30/0.60
24. *Pollichia campestris*	125	0.1	11	Has	Tsc	0.40
25. *Oldenlandia herbacea*	114	0.4	43	Has	Tsc	0.40
26. *Heteropogon contortus*	86	1.1	40	Hgp	Hsc	0.30/0.80
27. *Waltheria indica*	62	0.1	20	Hpd	Hsc	0.50
28. *Commelina africana*	22	0.1	19	Has	Tsc	0.20
29. *Terminalia sericea*	17	25.6	116	Tbd	Pmi	3.00
30. *Themeda triandra*	-20	0.9	28	Hgp	Hsc	0.60/1.00
31. *Becium angustifolium*	-92	1.3	16	Has	Tsc	0.40

[a] Number of occurrences in the strip of 200 quadrats.

Other pattern measurements

Results of other tests of pattern were not of much help in interpreting these two transects. For neither transect could a well-defined period be recognized from the periodicity search. For both transects the adjoining pairs test gave very high probabilities of contagion for species occurring in more than 5% of the quadrats, with few exceptions — *Phyllanthus burchellii, Mariscus laxiflorus*, and *Waltheria indica* in transect 6. Tests for scale of contagion of individual species gave generally weak results. For transect 2a a scale of 9–10 m was suggested for *Burkea* and *Ochna* clumps, but not for *Terminalia*; among other species a scale of 8 m was suggested for *Fadogia monticola*, around 10 m for *Justicia pallidior, Justicia anagalloides* and *Elionurus muticus*, a scale of 12–15 m for *Tristachya rehmannii* and *Eragrostis pallens*. For transect 6 a scale of 16–18 m may be weakly suggested for *Ochna*, but no scale for *Burkea* and *Terminalia*. For subordinate species, scales of 12–13 m were suggested for *Justicia minima, Commelina erecta,* and *Oldenlandia herbacea* and 16–17 m for *Eragrostis pallens*. As in transect 1, the tests for species association gave high probability of association (or negative association) by chi-square, but the values for the Cole index

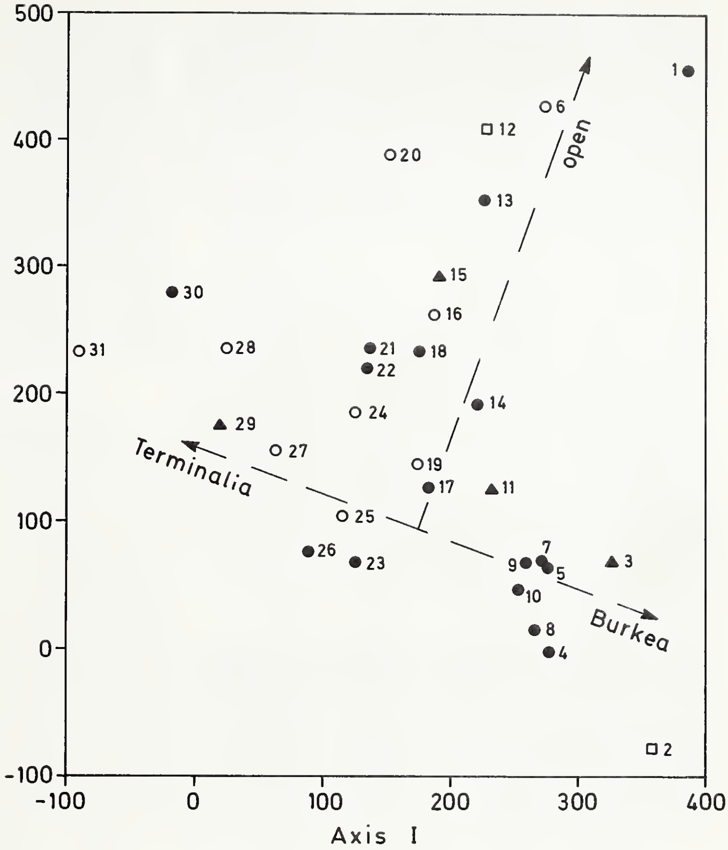

FIG. 15. — Ordination by DCA of 31 species of transect 6, a denser *Burkea africana–Terminalia sericea* woodland. Species numbers are given in Table 10. The *Burkea–Terminalia* gradient related to nutrient conditions (see Fig. 7) is oblique from lower right upward; the covered to open gradient is from lower left and center to upper right.

and percentage similarity of distribution suggested complex, multidirectional relations among species, expressed in mostly low or moderate association measures in which distinct groups of associates could not be recognized. Spectral analysis was not applied to transect 2 and seemed ineffective for transect 6.

Rocky soil patterns

Ordination

Transects 4 and 5 were taken on the slope and the almost-level summit, respectively, of a low sandstone hill, Maroelakop. On their rocky soils these woodlands differ significantly from the remaining transects of the study. Mean exposed rock cover is zero in the sandy soils of transects 1–3 and 6, about 60% for transect 4 on the slope of Maroelakop and 3.5% for transect 5 on its summit (Table 2). These transects were subjected to the same analyses as those on level and sandy terrain. First-axis species relationships are given in Tables 11 and 12.

In the ordinations of both transects there were marked changes in the relationships of species to the axes and one another for ordinations with different weightings, numbers of species, and with and without trees. In the ordinations of transect 4 using tree data (Fig. 16, EV's = 0.536, 0.417), five groups of species, of which four are characterized by tree species, are suggested: (1) *Combretum molle* with *Commelina africana* and other understory species; (2) *Diplorhynchus condylocarpon* with *Tragia rupestris, Enneapogon scoparius,* and other species; (3) *Combretum apiculatum* with *Phyllanthus burchellii,* etc.; (4) *Canthium gilfillanii, Lannea discolor* and *Burkea africana* as trees with *Schizachyrium sanguineum* and other species; and (5) *Tephrosia longipes, Heteropogon contortus, Corchorus kirkii,* etc. (no trees). The orientations of these groups on the axes and the associations of subordinate species with them varied from one ordination to another.

Somewhat more consistency appeared in the different ordinations of transect 5 (Fig. 17, EV's = 0.474, 0.388): in eight variant ordinations groups 1 and 2 among the following were at opposite ends of the first, and groups 3 and 4 at opposite ends of the second, axes. The groups suggested are: (1) *Burkea africana* and *Peltophorum africanum* as trees, with *Justicia protracta, Tagetes minuta, Rhynchelytrum setifolium, Commelina africana, Pollichia campestris, Schizachyrium sanguineum* and *Kalanchoe paniculata*; (2) *Lannea discolor* and *Dombeya rotundifolia* as trees with *Triumfetta sonderi, Schizachyrium jeffreysii, Brachiaria serrata, Justicia minima* and *Phyllanthus burchellii*; (3) *Combretum molle* and *Diplorhynchus condylocarpon* as trees with *Hyperthelia dissoluta, Eragrostis cilianensis, Sutera burkeana* and *Xerophyta retinervis*; (4) *Dichrostachys cinerea* and *Combretum zeyheri* as trees with *Lippia javanica, Brachiaria nigropedata, Rhynchelytrum villosum, Themeda triandra*, and in some ordinations *Elionurus muticus, Oldenlandia herbacea* and *Aristida diffusa;* (5) a central complex without trees, including the understory species *Trichoneura grandiglumis, Ipomoea transvaalensis, Pellaea calomelanos, Waltheria indica, Indigofera daleoides, Tephrosia longipes* and *Loudetia flavida.*

Efforts to relate the axes of the ordinations to recorded tree and rock cover per cents were unsuccessful, but tree cover increases from 37% to 76% (means of thirds of the quadrats as ordinated) along the diagonal from lower right to upper left in Fig. 16, transect 4. For species shared between the rocky-soil transects 4 and 5 and the remaining sandy-soil transects, the relationships to the ordination axes and to other species differ. Probably no simple consistency should be expected, if species responses are to soil factors and these factors differ widely between the two groups of transects, while species distributions are affected also by animal disturbance and chance establishment.

The relationships of species are, however, so variable among the different ordinations, especially of transect 4, as to raise the question of whether the ordination axes are responding to more than random differences in species occurrence. Evidence suggests that they are: (1) As with other transects, the matrix radomization tests support the significance of the first two DCA axes and imply that these represent significant directions of co-ordinated species responses, as distinguished from chance differences in species abundance (Fig. 4). (2) Comparing ordinations for transects 4 and 5, the pattern of occurrence of tree species in relation to the first two axes is similar (Figs 16 & 17). In both cases *Burkea africana* is high on the first axis and *Combretum molle* on the second. (3) A common herb axis is also suggested, extending from lower left toward upper right in the ordination field: *Heteropogon contortus, Brachiaria nigropedata, Phyllanthus burchellii, Commelina erecta, Oldenlandia herbacea, Tephrosia longipes, Pellaea calomelanos, Rhynchelytrum setifolium, Schizachyrium sanguineum* and *Commelina africana.* Four of these species are in roughly similar sequence in transect 6: *Heteropogon contortus, Commelina erecta, Oldenlandia herbacea* and *Commelina africana.*

Broader field observation of the behaviour of these species offers a provisional interpretation (G.K. Theron, pers. comm). The major species relationships are oblique to the ordination axes: from those adapted to shallow rocky soils on the upper left (*Eragrostis cilianensis, Combretum molle, Diplorhynchus condylocarpon, Grewia monticola* and *Xerophyta retinervis*) to those on deeper and leached soils on the lower right (*Combretum zeyheri, Lippia javanica*) (transect 5), or from shallow (and often sandy) soils on the upper left (*Diplorhynchus condylocarpon, Combretum molle* and *Tragia rupestris*) to deeper rocky soils on the lower right (*Canthium gilfillanii, Burkea africana* and *Lannea discolor*) (transect 4). The contrasting diagonal from lower left to upper right, to which the herb sequence mentioned relates, is probably from relatively more xeric to mesic. The scale on which these species and groups of species are mixed is small; the profiles of DCA scores show

TABLE 11. — Species characterization and distribution in a DCA ordination of transect 4, rocky-slope *Diplorhynchus condylocarpon — Lannea discolor* woodland

Species	Transect ranges 1	2	3	4	5	6	7	8	9	10	Score on DCA axis 1 (X 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
1. *Burkea africana*	[a]–	–	+	–	+	–	–	+	+	3	395	2.7	[b]10	Tbd	Pmi	3.00
2. *Rhynchosia longiflora*	–	–	+	+	+	+	–	+	+	+	338	0.1	14	Hpd	Hv	1.00
3. *Canthium gilfillanii*	+	+	+	1	+	+	2	1	1	1	276	6.7	103	Ssp	Pn	1.50
4. *Lannea discolor*	+	+	+	1	1	2	5	5	2	1	266	13.0	98	Tbd	Pmi	3.00
5. *Schizachyrium sanguineum*	+	+	–	+	+	+	+	+	+	+	197	1.5	45	Hgp	Hcs	0.40/0.9
6. *Tephrosia longipes*	+	+	+	+	+	+	+	+	+	+	179	0.1	35	Ssf	Pn	0.50
7. *Rhynchelytrum setifolium*	+	+	+	+	+	+	+	+	–	+	175	0.6	37	Hgp	Hcs	0.25/0.6
8. *Commelina africana*	+	+	+	+	+	+	+	+	+	+	174	0.4	74	Has	Tsc	0.20
9. *Pellaea calomelanos*	+	+	+	+	+	+	+	+	+	+	172	0.6	108	Hfd	Hsc	0.40
10. *Combretum molle*	+	+	+	–	+	–	+	1	1	1	168	3.3	20	Tbd	Pmi	3.00
11. *Commelina erecta*	+	+	+	+	+	+	+	+	+	+	142	0.1	27	Has	Tsc	0.15
12. *Barleria bremekampii*	1	1	1	1	+	+	+	1	+	+	133	6.5	107	Sbd	Pn	2.00
13. *Corchorus kirkii*	+	+	+	+	+	+	+	+	+	1	119	2.5	84	Ssf	Pn	0.40
14. *Enneapogon scoparius*	+	2	1	1	1	1	1	+	+	+	116	6.7	130	Has	Tsc	0.15/0.35
15. *Heteropogon contortus*	–	+	–	–	–	–	+	+	+	+	83	0.6	24	Hgp	Hsc	0.30/0.8
16. *Brachiaria nigropedata*	–	–	+	+	+	+	+	+	+	+	72	0.9	47	Hgp	Hsc	0.30/0.6
17. *Oldenlandia herbacea*	+	+	+	+	+	+	+	+	+	+	71	0.1	36	Has	Tsc	0.40
18. *Helichrysum cerastioides*	–	–	+	+	+	–	+	+	–	–	41	0.3	11	Hpd	Hsc	0.40
19. *Diplorhynchus condylocarpon*	8	9	9	7	2	+	+	+	+	+	38	24.2	96	Tbd	Pmi	3.00
20. *Phyllanthus burchellii*	–	+	–	+	+	+	–	+	–	+	37	0.1	12	Has	Tsc	0.20
21. *Tragia rupestris*	+	+	+	–	+	–	–	+	+	–	-50	0.1	11	Hpd	Hv	1.00
22. *Eragrostis lehmanniana*	–	+	+	+	–	+	–	–	+	–	-71	0.2	11	Hgp	Hsc	0.60/0.9
23. *Combretum apiculatum*	1	5	+	+	+	–	–	–	+	–	-72	5.3	20	Tbd	Pmi	3.00
Mean number of species per quadrat in composite	5.0	6.5	5.8	6.3	6.8	6.6	6.5	6.6	6.7	6.9						

[a] Mean cover deciles in sets of 20 quadrats as ordinated.
[b] Number of occurrences in strip of 200, 1-m² quadrats.

TABLE 12. — Species characterization and distribution in a DCA ordination of transect 5, rocky summit *Burkea africana–Lannea discolor* woodland

Species	Transect ranges										Score on DCA axis 1 (X 100)	Average cover %	Total frequency	Growth form	Life form	Mean height
	1	2	3	4	5	6	7	8	9	10						
1. *Peltophorum africanum*	[a]6	+	–	+	–	–	–	–	–	–	492	3.6	[b]10	Tbd	Pmi	3.00
2. *Justicia protracta*	+	+	–	+	–	+	–	–	–	–	482	0.1	14	Has	Tsc	0.20
3. *Tagetes minuta*	+	+	+	–	–	–	–	–	–	–	450		13	Has	Tsc	0.40
4. *Combretum zeyheri*	4	1	–	+	–	–	–	–	–	–	446	3.0	10	Tbd	Pmi	3.00
5. *Lippia javanica*	1	+	–	–	–	+	–	+	+	+	420	0.9	10	Hpd	Hsc	1.00
6. *Commelina africana*	+	+	+	+	+	+	+	–	+	+	409	0.1	28	Has	Tsc	0.20
7. *Rhynchelytrum setifolium*	+	+	+	+	+	–	+	+	+	–	406	0.6	38	Hgp	Hsc	0.25/0.6
8. *Digitaria eriantha*	+	+	+	–	+	+	+	+	–	+	402	0.2	18	Hgp	Hsp	0.20/0.3
9. *Burkea africana*	9	9	4	+	+	+	+	+	+	+	396	13.4	42	Tbd	Pmi	3.00
10. *Pollichia campestris*	+	+	+	–	–	–	+	–	+	+	357	0.1	16	Has	Tsc	0.40
11. *Schizachyrium sanguineum*	+	3	+	1	+	+	+	+	+	+	340	4.6	59	Hgp	Hsc	0.40/0.9
12. *Mariscus laxiflorus*	+	+	+	+	+	+	+	+	+	+	337	0.3	47	Hgp	Hsc	0.30/0.5
13. *Dichrostachys cinerea*	+	1	+	–	+	+	+	–	–	–	332	1.2	14	Tpl	Pmi	3.00
14. *Kalanchoe paniculata*	+	+	–	+	+	+	+	–	+	+	331	0.2	20	Ssf	Csu	0.80
15. *Solanum panduriforme*	–	+	–	+	+	+	+	+	+	+	326	0.1	23	Hpd	Csf	0.30
16. *Barleria bremekampii*	+	+	+	+	+	+	+	+	+	+	314	0.5	121	Sbd	Pn	2.00
17. *Themeda triandra*	1	2	2	1	1	1	2	+	1	+	290	8.6	143	Hgp	Hsc	0.60/1.0
18. *Hyperthelia dissoluta*	+	+	1	+	+	+	+	+	–	–	287	2.1	24	Hgp	Hsc	1.50/2.0
19. *Pellaea calomelanos*	+	+	+	+	+	+	+	+	+	+	273	0.6	125	Hfd	Hsc	0.40
20. *Elionurus muticus*	+	+	+	+	+	+	+	+	+	+	256	0.9	48	Hgp	Hsc	0.30/0.6
21. *Ipomoea transvaalensis*	+	+	+	+	+	+	+	+	+	+	250	0.2	62	Has	Tsc	0.40
22. *Heteropogon contortus*	+	+	+	+	+	+	+	+	+	+	249	3.2	91	Hgp	Hsc	0.30/0.9
23. *Waltheria indica*	+	+	–	+	+	+	+	+	+	+	242	1.0	58	Hpd	Hsc	0.50
24. *Brachiaria nigropedata*	+	+	+	+	+	+	+	+	+	+	226	1.6	62	Hgp	Hsc	0.30/0.6
25. *Aristida diffusa*	+	+	+	+	+	+	+	+	+	+	222	1.2	42	Hgp	Hsc	0.75/1.0
26. *Xerophyta retinervis*	+	+	+	+	+	2	+	+	+	+	212	3.4	58	Sr	Pn	1.00
27. *Oldenlandia herbacea*	+	+	+	+	+	+	+	+	+	+	211	0.2	47	Has	Tsc	0.40
28. *Indigofera daleoides*	+	+	+	+	+	+	+	+	+	+	207	0.1	28	Ssf	Pn	0.50
29. *Fimbristylis hispidula*	+	+	+	+	+	+	+	+	+	+	196	0.5	82	Hgp	Hsc	0.20/0.3
30. *Trichoneura grandiglumis*	–	+	+	+	+	+	+	+	+	+	193	0.3	22	Hgp	Hsc	0.08/0.2
31. *Tephrosia longipes*	+	+	+	+	+	+	+	+	+	+	174	0.2	58	Ssf	Pn	0.50
32. *Sutera burkeana*	–	+	+	+	+	+	+	+	–	–	169	0.4	28	Has	Tsc	0.20
33. *Loudetia flavida*	+	1	2	+	3	2	2	3	3	1	155	11.4	142	Hgp	Hsc	0.25/0.6
34. *Diheteropogon amplectens*	+	+	+	+	1	1	+	1	1	1	144	5.5	155	Hgp	Hsc	0.80/1.2
35. *Combretum molle*	–	+	+	+	–	+	+	+	–	+	115	0.2	10	Tbd	Pmi	3.00
36. *Phyllanthus burchellii*	+	–	+	–	–	–	+	+	+	+	103		12	Has	Tsc	0.20
37. *Commelina erecta*	–	+	+	+	+	+	+	+	+	+	102	0.3	44	Has	Tsc	0.15
38. *Rhynchelytrum villosum*	–	–	+	+	+	–	+	+	+	+	92	0.4	38	Hga	Tsc	0.40/0.6
39. *Clerodendrum triphyllum*	–	+	–	+	+	+	+	+	+	+	91	0.2	16	Hpd	Hsc	0.50
40. *Lannea discolor*	+	+	+	1	+	2	3	4	4	6	82	12.4	71	Tbd	Pmi	3.00
41. *Eragrostis cilianensis*	–	+	+	+	+	–	+	+	+	+	70	0.4	19	Hgp	Hsc	0.15/0.4
42. *Grewia monticola*	–	+	+	–	+	+	+	–	+	1	69	2.2	11	Sbd	Pmi	2.25
43. *Justicia minima*	+	+	+	+	+	+	+	+	+	+	67	0.4	73	Has	Tsc	0.20
44. *Brachiaria serrata*	–	–	+	+	+	+	+	+			60	0.6	18	Hgp	Hsc	0.20/0.5
45. *Schizachyrium jeffreysii*	–	+	+	–	–	+	+	+	1	2	48	3.0	33	Hgp	Hsc	0.25/0.5
46. *Diplorhynchus condylocarpon*	+	+	+	–	+	+	+	+	1	1	37	1.5	24	Tbd	Pmi	3.00
47. *Triumfetta sonderi*	–	–	–	+	+	+	+	+	+	2	-25	2.0	22	Ssf	Pn	0.75
Mean number of species per quadrat in composite	10.9	9.9	9.3	9.1	9.1	9.4	9.4	9.8	10.0	9.6						

[a] Mean cover deciles in sets of 22–23 quadrats as ordinated.
[b] Number of occurrences in strip of 225, 1-m² quadrats.

rapid and irregular fluctuation without evident pattern (which may then be sought also in the other pattern measures and spectral analysis).

Other pattern measurements

The supplementary pattern measurements were of little help with the interpretation. The search for periodicity gave apparently negative results in both transects. The adjoining pairs tests gave the usual high probabilities of departure from randomness for most species in both transects. No scale of contagion was indicated for any species in transect 4. In transect 5 the tests suggested scales of contagion at 9–10 m for *Barleria bremekampii, Heteropogon contortus, Brachiaria nigropedata, Schizachyrium sanguineum* and *Mariscus laxiflorus*. This scale seemed not effectively related to tree cover or other environmental factors. Although chi-square tests for co-occurrence were highly significant for some pairs of species in both transects, well-defined groups of associates could be recognized in neither.

Spectral analysis

For transect 4, five most abundant species were selected for analysis: *Enneapogon scoparius, Pellaea calomelanos, Barleria bremekampii, Canthium gilfillanii* and *Lannea discolor*. The transect was 200 m long, permitting reasonable resolution of wavelengths up to perhaps 50 m. There were not nearly so many species in this transect

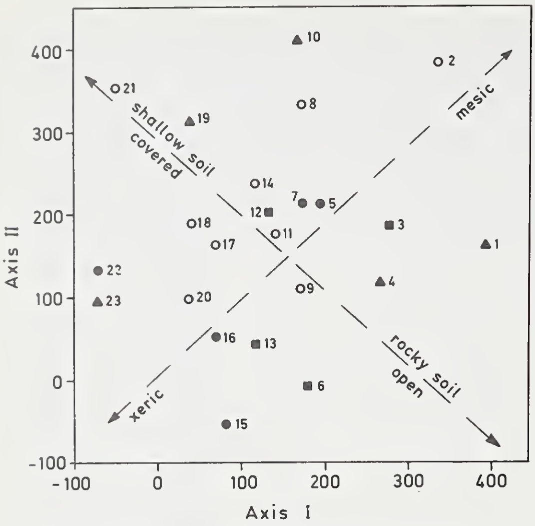

FIG. 16. —Ordination by DCA of 23 species of transect 4, a rocky-slope woodland dominated by *Diplorhynchus condylocarpon* and *Lannea discolor.* Species numbers are given in Table 11. Apparent soil pattern gradients are diagonal, as indicated.

as in transect 1, and the selected species were of comparable variance. The first four species named had variances from 1.5 to 1.75. The last, *Lannea discolor*, had a higher variance, 2.5.

None of the species yielded very distinct correlograms or spectra, but all showed peaks in their correlograms at lags between 5 and 8 m, and all showed roughly corresponding peaks in their power spectra at wavelengths between 4 and 7 m. Accordingly, frequency domain PCA was performed at two frequencies, 0.16667 m^{-1} and 0.12500 m^{-1}, in the hope of deciding whether the pictures that would emerge at the two wavelengths, 6 m and 8 m, were indicative of a single underlying pattern.

At both frequencies, when eigenanalysis was carried out without any standardization the first eigenvector showed simply an overwhelming contribution from *Lannea discolor*, the species with the greatest variance (Fig. 18A) and no definite influence due to the other species. The second eigenvector (Fig. 18B) showed strong contributions from *Barleria bremekampii* and *Canthium gilfillanii*, out of phase with each other, and with *Enneapogon scoparius* about 90° out of phase with each. At the two frequencies, corresponding to 6 m and 8 m wavelengths respectively, the first eigenvector accounted for 39% and 36% of the variance, and the second eigenvector accounted for 30% and 33%. These differences between the first and second eigenvalues are

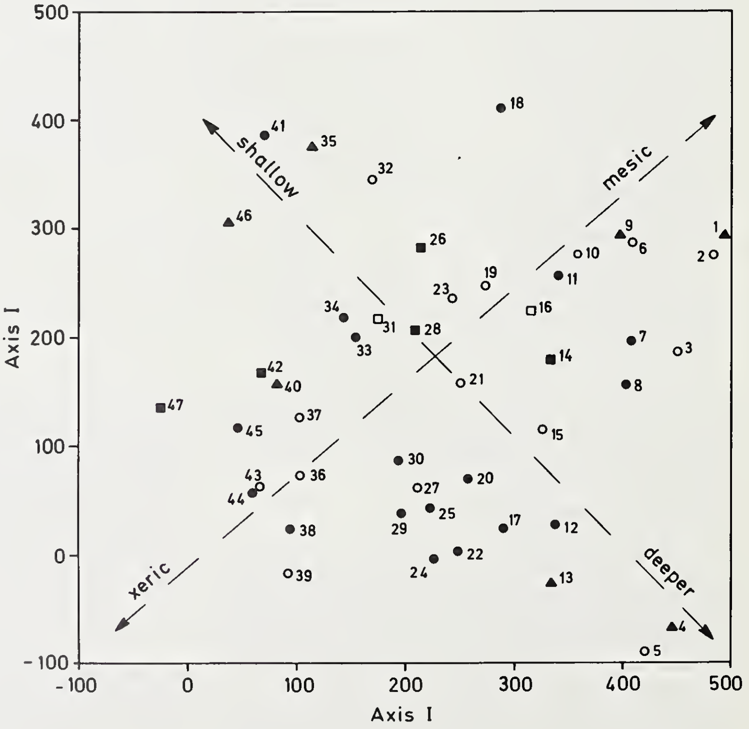

FIG. 17. — Ordination by DCA of 47 species of transect 5, a rocky-soil summit woodland dominated by *Burkea africana* and *Lannea discolor*. Species numbers are given in Table 12.

quite small, so it is fortuitous if the eigenvectors yielded to parsimonious interpretation. As it is, the analysis indicates an alternation of *Barleria bremekampii* and *Canthium gilfillanii* every 3 or 4 m, with *Lannea discolor* patches appearing at 6 or 8 m intervals but without regard for the *Barleria bremekampii–Canthium gilfillanii* pattern. The eigenvectors from the 6 m analysis are shown in Fig. 18.

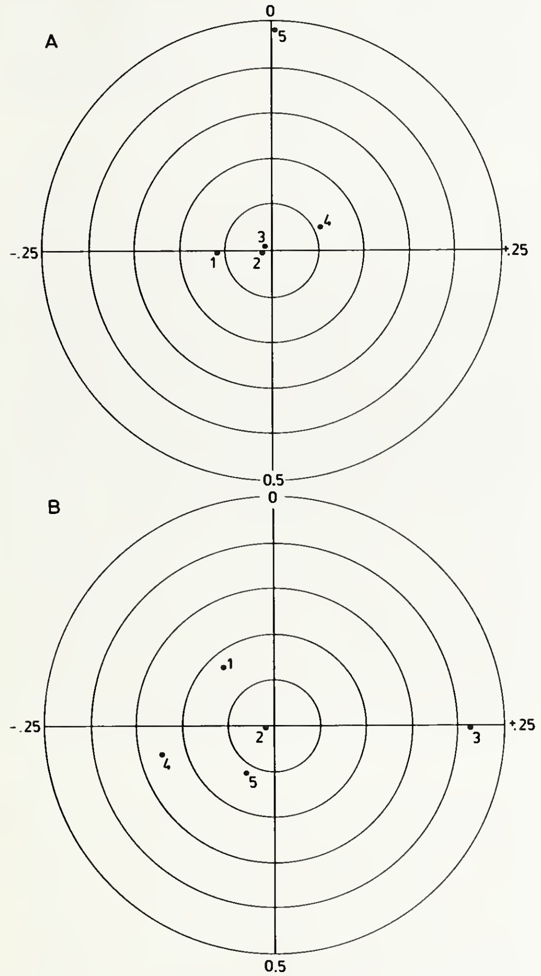

FIG. 18. — Frequency domain PCA for 5 species of transect 4 using cover data without standardization, with a wavelength of 6 m: A, first eigenvector; B, second eigenvector. Species numbers: 1 = *Enneapogon scoparius*; 2 = *Pellaea calomelanos*; 3 = *Barleria bremekampii*; 4 = *Canthium gilfillanii*; 5 = *Lannea discolor*.

When the matrices of cross spectra were normalized to unit power in all species, thus removing the dominance due to the higher variance of *Lannea discolor*, some elements of this same pattern remained. The out-of-phase relationship between *Barleria bremekampii* and *Canthium gilfillanii* now appeared in the first eigenvector of the 6 m wavelength analysis. In both cases, *Enneapogon scoparius* continued to contribute strongly to the pattern at a somewhat different, intermediate, phase angle, though more closely aligned with *Canthium gilfillanii*. There was less in common in the complementary eigenvectors. Both showed *Canthium gilfillanii* and *Enneapogon scoparius* as contributing strongly out of phase, but the phase relationships of the remaining species were inconsistent.

On balance, the consistency with which wave structures involving *Barleria bremekampii* and *Canthium gilfillanii* (180° out of phase) and *Enneapogon scoparius* (90° out of phase) were indicated in these analyses suggests that there was indeed such an alternation between *Barleria bremekampii* and *Canthium gilfillanii* about every 3 m with *Enneapogon scoparius* interspersed less regularly. The other species examined concurred in showing some tendency toward spectral peaks at about this same wavelength, but they seemed not to be patterned strongly in response to each other or with respect to the wave structure of *Barleria bremekampii* and *Canthium gilfillanii*. Biological interpretation is difficult. It can only be suggested that rockier soils and species adapted to them (*Canthium gilfillanii* and *Pellaea calomelanos*) alternate with less rocky soils and corresponding species (*Barleria bremekampii, Enneapogon scoparius*) in a pattern repeating every 6 m, whereas *Lannea discolor* occurs as a dominant in both phases with little relation to this pattern. Observation of the slight topographic undulation on the hillside is consistent with this suggestion, but the 6 m period could not itself be recognized in the field.

Five most abundant species in transect 5 were also selected for analysis: *Diheteropogon amplectens, Themeda triandra, Loudetia flavida, Pellaea calomelanos,* and *Barleria bremekampii*. This transect, like transect 4, had fewer species than the *Burkea* savannas, but even among the five species variances of the log cover values differed by an order of magnitude.

Only *Themeda triandra* yielded a distinct correlogram with a peak at 17 m lag. Its power spectrum, on the other hand, showed a distinct peak at about a 3 m wavelength, with the 17 m variance being absorbed simply into a very red spectrum which peaked at zero frequency. The other species all showed local peaks in their power spectra at wavelengths between 3 and 5 m, but these did not correspond to clear peaks in their respective correlograms. Instead they depended on alignment of very small repeated peaks and shoulders in the correlogram. This evidence of a persistent but quite weak 'signal' at about a 3 m wavelength may have been due to a genuine pattern, such as undulation in microtopography or soil character on this scale; but it was not recognizable in the field and cannot be given biological interpretation.

Relationships among the transects

Two-way indicator species analysis (Twinspan) and DCA ordination were used to compare the transects with one another as samples representing major types in a landscape of vegetation. For this purpose transect 2 was divided into its 2a (*Burkea*) and 2b (*Acacia*) sections, and three sections each 300 m long were taken from transect 1 for comparison with other transects 200–300 m long. The resulting species lists were classified and ordinated using frequency per cents for 62 species occurring in more than 2, and 151 species occurring in more than 1 of the 9 transects and sections.

The numerical classification by Twinspan divided and grouped the strips much as might be expected. The first division separated the rocky-soil transects 4 and 5 from the remaining sandy-soil samples. *Brachiaria nigropedata, Combretum molle, Lannea discolor,* and *Schizachyrium sanguineum* are important indicator species for the rocky-soil samples that were also recorded in at least one other transect. The second division separated the two *Acacia* communities, transects 3 and 2b, from the remaining sandy-soil *Burkea* samples. *Aristida congesta, Eragrostis lehmanniana, Dichrostachys cinerea,* and *Pollichia campestris* are species important in the *Acacia* samples but occurring in some other transects. A third division separated transect 6 from the remaining, less dense *Burkea* savannas, and a fourth division separated transect 2a from the three sections of transect 1. Species most widespread in this vegetation pattern, as expressed by occurrence in all 9 transects and sections, were *Waltheria indica, Commelina erecta* and *Heteropogon contortus*; several other species occurred in 6 or 7 of the sections — *Digitaria eriantha, Elionurus muticus, Justicia minima, Evolvulus alsinoides, Solanum panduriforme, Commelina africana, Themeda triandra, Phyllanthus burchellii, Mariscus laxiflorus* and *Burkea africana.*

The DCA ordination using 151 species is shown in Fig. 19. The first axis separates the rocky-soil transects at one extreme from the *Acacia* samples at the other, with the *Burkea* samples in the middle. The axis apparently represents different combinations of soil effects — increased fertility on sand toward the *Acacia* communities, vs more extreme soil conditions on the leached, rocky soils on Maroelakop. The second axis separates from the open *Burkea* savannas the denser *Burkea* woodland of transect 6, on a soil with higher content of fine particles than transect 1. The three strips of transect 1 are closely clustered; the parts of that transect are very much alike relative to the other vegetation sampled, despite the gradual catena along part of which transect 1 extended.

The ordination is consistent with a view of the landscape. The relatively open *Burkea–Terminalia* savannas seem both central to and prevalent in the vegetation pattern of the area. From this prevailing or matrix community-type other communities depart in three major directions: (a) toward rocky soils where these outcrop on Maroelakop and other hills, (b) down the catena through denser phases of *Burkea* woodland to the open marshes or vleis, and (c) within the matrix toward *Acacia* savannas where effects of disturbance persist. Being central and prevalent, the *Burkea–Terminalia* savannas may be considered (if they are also relatively stable) the prevailing climax for the area.

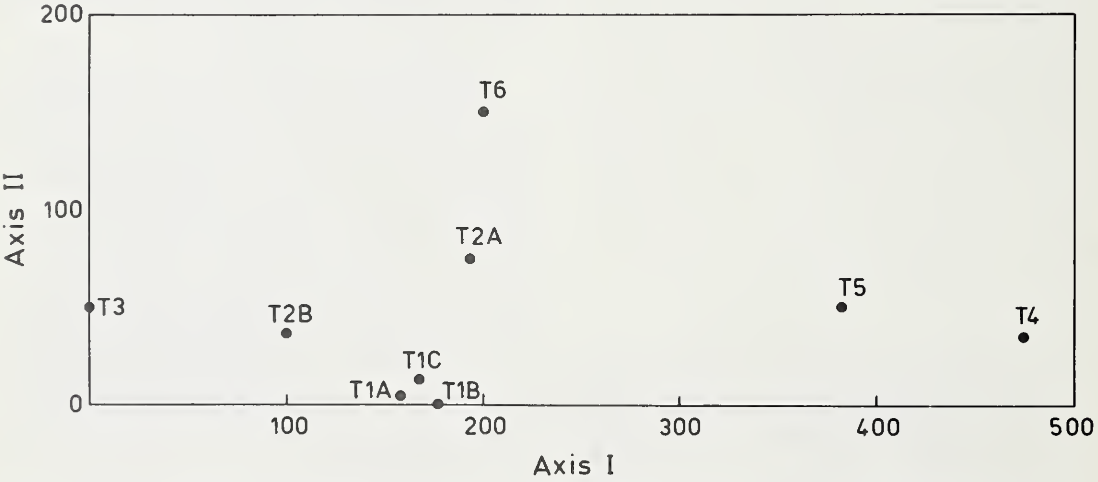

FIG. 19. —A DCA ordination of the Nylsvley transects, using 151 species. Transect 2 is divided into the unburned *Burkea africana* savanna (Tr. 2A) and *Acacia karroo* patch (Tr. 2B), transect 1 is divided into equal-sized thirds (T1A, T1B, T1C) from bottom to top of transect. Transect 1 is the central or prevailing savanna-woodland vegetation for the area, with other types diverging toward rocky soils (Tr. 5 and 4), denser cover (Tr. 2 and 6), and disturbance (*Acacia* savannas, Tr. 2B and 3).

Discussion

Method

Three groups of techniques were used for the Nylsvley pattern analyses: (a) techniques that, with variants not used here, have made up traditional pattern analysis (Greig-Smith, 1964, 1979; Kershaw, 1973) — tests for contagion and scale of contagion, species association and correlation — together with periodicity search based on community indices (PS, CC, and ordination scores), (b) spectral analysis as recently applied to problems of species and community periodicity and scale (Platt & Denman, 1975; Ripley, 1978), together with frequency domain principal components analysis (Wallace & Dickenson, 1972; Goodman, 1980) and (c) ordination of small quadrats as an approach to recognizing major directions of variation in species composition and species response in community patterns (Whittaker *et al*., 1979a,b; Shmida & Whittaker, 1980; Whittaker & Naveh, 1980). The three should be complementary, but the Nylsvley study suggests some comments on their use and effectiveness.

It is familiar that most species in natural communities are contagiously distributed. Measurements are easily applied to demonstrate contagion and suggest scale for individual species. It seems difficult, however, to obtain results on how species relate to a community pattern with these measures; even with well-defined patterns the measures of scale may give only weak indications of community pattern (Whittaker *et al*., 1979b). Indices of contagion that may be used to seek scale — chi-square, $\sigma^2/\overline{x}$, $\sigma/\overline{x}$, $(\sigma^2-\overline{x})\overline{x}^2$ (Hill, 1973a), and the Morisita (1959) index — give generally inconclusive results, often inconsistent from one index to another for a given species, indecisively suggesting a dispersion of different possible scales for different species in the same pattern. It is not clear that these measures give better recognition of pattern than visual scanning of transect data.

Searches for community-level periodicity based on percentage similarity and coefficient of community have given generally weak and marginal results. Ordination scores seem much more effective in indicating a scale of repeating compositional change in a community along a transect. When measures of species association or correlation are applied to a few species, these measures of relative distributional similarity can be useful for ordinations of species (McIntosh, 1973, 1978). With a large number of species, as in the Nylsvley transects, a large matrix of associations of all degrees but mostly weak or neutral is obtained; it is difficult to extract understanding of pattern from such matrices. With complex data, species are apparently better ordinated by dual techniques (ordinating both samples and species) such as reciprocal averaging and detrended correspondence analysis, rather than by techniques such as secondary reciprocal averaging and nonmetric multidimensional scaling that use only distance measures for species (Gauch *et al*., 1981).

In some applications the traditional techniques have given impressive results (Greig-Smith, 1979). For our study, however, the traditional measures were judged to be poor tools for constructing an understanding of community-level pattern. They are better regarded as supplementary, as providing some additional information that may be interpreted on the basis of ordination (Whittaker *et al*., 1979b). The tests for contagion and scale of individual species may be most useful for simple communities, for those in which the small number of species or occurrence of empty quadrats limits ordination, and for cases in which species distributions do not show co-ordinate response to major pattern factors.

Correlograms and power spectra seem stronger techniques for the recognition of individual species patterns (cf. Ripley, 1978; Goodman, 1980). The assumption of sinusoidal form limits the application of power spectra in ecological data; but use of power spectra and correlograms together gave effective results for some species in the present study. Cross spectra examine relations of pairs of species and can provide information — especially on lags of species distributions — that is not available from ordinary measurements of species association. Frequency domain principal components analysis (PCA) is related to, but different in function from, other ordinations. It asks how, at a given wavelength, species are distributed in relation to one another — as individual species or groups that occur with different intensities of relationship and are in phase, or out of phase, or partly out of phase.

The correlograms and power spectra, cross correlations and cross spectra, and frequency domain PCA therefore represent a sequence of techniques for analysis of single species, pairs and sets. For the major tree and herb species of transect 1, the cross spectra and frequency domain PCA gave results on spacing and alternation of species that were not accessible from the other techniques and not simply recognizable in the field data. Spectral analysis and related techniques are ineffective unless there is some periodicity inherent in the pattern. We judge that for patterns with some periodic quality these techniques have greater potential than the traditional ones, and can in some cases offer information on pattern that is not visually detectable and not available from ordination.

For quadrat ordination, not PCA but reciprocal averaging (RA) or detrended correspondence analysis (DCA) is appropriate. PCA, with its assumption of linear correlation, is valid for analysis of species relationships at a given frequency, but not for the curvilinear and nonmonotonic full distributions of species along ecological gradients (Gauch *et al.*, 1977). RA has been very effective for analysis of some strongly differentiated two-phase patterns (Whittaker *et al.*, 1979a,b; Shmida & Whittaker, 1980; Whittaker & Naveh, 1980). RA is little subject to the involution of axis extremes that afflicts PCA applied to ecological data. RA is, however, affected by some curvilinear distortion of higher axes, and somewhat distorted spacing of samples and species along axes. DCA corrects for both these limitations of RA (Hill, 1979a; Hill & Gauch, 1980). With easy cases of clear patterns, such as the *Acacia* communities, RA was an effective ordination but DCA was better, particularly as regards scaling of sample and species positions along axes. Given complex and difficult data, such as those for the other transects, RA did not give interpretable results, whereas some versions of DCA did so. For indirect ordination of difficult ecological data, DCA seems as much an advance over RA as RA was over PCA. Among the variant DCA ordinations tested, standardization by species maxima with rare species eliminated was most successful for these pattern analyses. This data treatment apparently best uses all information available for adequately represented species, while avoiding overemphasis of dominant species. Results were generally similar (i.e., first and second axes corresponded) for DCA ordinations with and without trees (see also Shmida & Whittaker, 1980).

The great strength of ordination for pattern analysis is that it can pick out directions of community differentiation, directions of co-ordinated species responses, in the pattern. No other technique does this with comparable efficacy. Frequency domain PCA can pick out major directions of community differentiation at a given wavelength; but DCA and RA use the whole body of information to detect axes of community differentiation, and this detection is not hampered by lack of periodicity in the data. Ordination by RA or DCA is then the more general technique for recognizing overall community pattern differentiation, frequency domain PCA for more detailed study of spacing and phase relationships among sets of species. For pattern analysis by DCA or other ordination to be effective there must be (a) a pattern of significantly co-ordinated species occurrences, (b) rich enough in species that these provide adequate information for ordination, and for which (c) there is a sample size both large enough to contain several species and small enough to distinguish the different parts of the pattern. For the present study 1-m² quadrats seemed appropriate to give significant first and second axes. Third and higher axes were generally determined by particular uncommon species and combinations of these; these axes, whether expressing chance species occurrences or disturbance or other local microenvironments, were seldom interpretable with the information available.

Both limitations and possibilities of these techniques involve the nature of 'pattern'. Pattern is not a unitary phenomenon but a congeries of different (though often interrelated) relationships on the levels of populations and communities (Whittaker & Levin, 1977). Let within-community pattern mean in general departure from randomness in the distribution of individual species and combinations of species. Then, questions at the level of the individual species population include: (a) degree of contagion (or regularity), (b) scale of contagion–area of clusters, (c) scale of contagion–spacing or frequency of clusters, (d) relative regularity or periodicity of clusters, (e) relative boundedness of clusters, and (f) means (and dispersions) of numbers of individuals in clusters. For pairs of species, questions are: (a') the degree of association or co-contagion, and (b') area and (c') frequency of joint patches, (d') relative regularity of co-occurrence, (e') boundedness of joint patches, (f') relative densities of the two species, and (g') lag and phase relations in their periodicity, if any. On the level of the community pattern the questions are: (a") degree of pattern differentiation, of contrast in species composition in samples (pattern diversity), (b") size, (c") frequency, (d") relative periodicity, and (e") relative boundedness of several-species patches, (f") means (and dispersions) of numbers of species in patches, and (g") phase relations among sets of species. The last implies, as a further key character, (h") the degree of co-ordination, or correlation in response vs independent and random occurrence, of the species. It is accepted that the species are individualistic in their responses. By co-ordination we mean here the degree to which species responses to pattern factors are, though individualistic, consistent and determinate (as coenoclines of population rise and fall along pattern axes) vs forming patches that may be well-defined but bear no consistent relationship to one another. The degree of pattern differentiation (a") and the degree of species co-ordination in response to the major pattern gradients (h") are partly independent.

No technique of pattern analysis can cope with more than one or a few of these. Traditional contagion measurement deals with (a) and, not always effectively, with (b) and (c). The techniques grouped here with spectral analysis can deal more effectively, for patterns that are to some degree periodic, with (b), (c), and (d) by correlograms and power spectra, with (b'), (c'), and (d') by cross spectra, and with (b"), (c"), and (d") by frequency domain PCA. Ordination permits approaches to (b"), (c"), and (g") by profiles of ordination scores along transects, and (d") by use of ordination scores for periodicity search. From eigenvalues, and other approaches to the ordinated data, pattern diversity (a") may be estimated. Ordination scores for quadrats can be used to measure relative boundedness, (e") (Whittaker *et al.*, 1979b); and ordinated scores of species, and relative richness of ordinated quadrats, can give expressions for (f").

Critical to the effectiveness of the ordination approach is point (h"). If, despite strongly developed contagion, species occurrences are random or uncoordinated relative to one another, ordination is ineffective. It should be noted that ordinations of data in which species patterns are uncoordinated (e.g., the data randomized within rows) can give eigenvalues large enough to suggest significant results. Comparison of eigenvalues for actual data with those for the same data randomized provides some indication of the degree of co-ordination, or significant directional differentiation, in species responses and community composition. Experience with such tests suggests that they are more useful for this question than as measures of relative effectiveness of different ordinations.

The major problems of pattern analysis are not with clearly defined patterns and strongly co-ordinated species responses. For such patterns and appropriate sample sizes it is relatively easy to obtain effective ordination. The results do not 'reveal' the pattern, but they do provide much information on sample relationships, species responses, and characteristics of the pattern that visual observation does not give. If the pattern is to some degree periodic, spectral analysis and related techniques also may be easily successful and may indicate species relationships not otherwise recognizable. Striking two-phase patterns are, however, the easy cases for such pattern analysis; the real tests for techniques are offered by patterns that are relatively complex, obscure, and uncoordinated. Patterns in which species distributions are quite uncoordinated may be resistant to any technique except simple measurement of contagion. The Nylsvley non-*Acacia* patterns are relatively difficult combinations of significant co-ordination in relation to major factors with a high degree of irregularity in species response to these and other, unknown factors. Such combinations may be more common than either strong two-phase co-ordination, or non-co-ordination of pattern. In dealing with the relatively complex and difficult patterns at Nylsvley, ordination was able to assume its heuristic role (Whittaker & Gauch, 1978) — revealing directions of community response that had not been recognized, but could be tested and interpreted with other data applied to the ordination results. Success with complex patterns may depend on care, effort, supporting data and broader knowledge of species responses. Both these needs and a principal purpose — revealing and summarizing pattern — are general for ordination as a research method.

Character of the pattern

In all the transects (except the two on rocky soils) the first axis of pattern differentiation led from shaded to open quadrats, as in other studies of vegetation with an open woody stratum (Whittaker *et al.*, 1979a,b; Whittaker & Naveh, 1980). It is understood that this first axis is not simply one of light intensity, but is a complex-gradient of many microclimatic and soil factors. Along the second axes in the *Burkea* savannas, soil nutrients are apparently of primary importance. On rocky soils, transects 4 and 5, soil depth appeared to be a principal determinant of pattern (cf. Bratton, 1976a,b), with soil moisture as a second axis.

Second axes in the *Acacia* savannas, transects 2b and 3, and third and higher axes in the *Burkea* savannas are apparently determined by factors related to disturbance. Some of these — animal burrowing and fertilization by animal faeces — also act through effects on the soil. Soil factors are likely also to be of much importance along the first, open-to-cover axes, because of effects of the trees on soil organic matter and nutrient levels. Soil factors are thus probably paramount in all the patterns examined. In transect 1 the texture analyses of soil samples did not reveal consistent differences in particle size spectra that could be related to the *Burkea* and *Terminalia* clumps. We cannot exclude the possibility that differences in soil fertility, pre-dating the present vegetation, influenced the location of trees vs openings and of *Burkea* vs *Terminalia*. Savanna trees can, however, enrich the soil by pumping of nutrients from deeper in the soil (and openings into which their roots extend), or by accumulation of nutrients from precipitation and contribution of these nutrients to the soil in litter (Kellman, 1979). It seems likely that, within individual savanna transects, the locations of trees have determined small-scale soil nutrient differences rather than being determined by such differences.

Beyond the over-all significance of soils, two observations are suggested — the importance of nutrients and the importance of biological determination of the patterns. On these old, leached, sandy, nutrient-poor soils, apparently modest differences in soil nutrients can be highly significant to plants and they may persist for some time by cycling of nutrients through litter. Apart from the *Burkea–Terminalia–Acacia* axis in transect 1, persistent enrichment is the probable reason for the *Acacia* savannas as large patches in the over-all pattern of the *Burkea* savanna landscape. Among nutrients added to the soil by human occupation, fertilization, and penned livestock, phosphorus and others may persist by retention in plants and tight cycling back into plants through mycorrhizal uptake on a nutrient-poor soil (cf. Stark & Jordan, 1978). In a deciduous forest in the United States, past Indian encampment was indicated by local higher phosphorus concentrations in the soil long after return of the encampment to apparently undisturbed forest (Gauch & Stone, 1979). A major feature of the Nylsvley patterns is the responsiveness of the vegetation to nutrients at different levels of vegetation pattern — the long and very gently sloping catena affecting transect 1, the larger-scale differences appearing in the *Acacia* patches, and the smaller-scale effects of individual trees in both *Burkea* and *Acacia* savannas.

Much of the pattern of the sandy-soil savannas is thus determined by biological modification of plant microhabitats, or microsites. Microsite modifications by the trees include shade, microclimate, and soil effects, all of which may differ between tree species, as well as with size of trees and differing species and densities of woody undergrowth. Among the soil effects that differ between species are nutrient accumulation and turnover and unknown, but possible, allelopathy. The physiognomic structure of the savanna — tree and tree-shrub clumps of differing sizes, species and species combinations, and cover densities dispersed in a grassland matrix with tree roots and litter effects extending outside the clumps into openings — thus produces a complex pattern of biological modification of microsites for understory plants and woody seedlings. So far as we can establish, the patterns within particular savanna stands on sandy soils are primarily consequent on biological modification of microsites, those on the rocky soils on physical characteristics — soil depth and moisture supply — of microsites. To borrow terms from the study of succession, the patterns on sandy soils vs rocky soils are primarily autogenic and allogenic, respectively.

With the effects of plants on the sandy soils should be included effects of the abundant animal life of the savanna. These effects — termite mounds, burrows, castings, excavations for underground food, urination, dung heaps (some largely removed and buried by scarabs and others not), favouring by animals of particular clumps or openings and trampling — impose on an already complex pattern a further level of complexity in local modifications, mostly on a smaller scale, affecting plant establishment and survival. We are unable to deal with these animal effects beyond the most obvious, such as the different flora on termite mounds (which were not sampled in this study). We infer, however, that the strongly irregular or random quality that seems superimposed on the pattern as interpreted in terms of woody cover and dominant species, is partly consequent on these many modifications of plant microsites by animals.

Microsites and community maintenance

While it is not possible to analyse the full complexity of the pattern, it may be possible to interpret the manner in which a rich community maintains itself. In relatively stable communities a species population is maintained by a steady-state turnover, aspects of which are density of seeds, frequency of seeds in suitable seedling microsites, per cent germination, survival and growth to reproductive age (as affected by resource use, competition, predation, symbiosis and environmental hazard) and density of seeds that the population of surviving, mature plants sheds on the microsite mosaic (Whittaker, 1969, 1975; Harper & White, 1971; Harper, 1977; Whittaker & Levin, 1977). A key factor for the population is the presence and frequency of microsites relatively favourable for the germination and survival of seedlings of that species, microsites representing relatively 'safe sites' (Harper, 1977) or 'regeneration niches' (Grubb, 1977) for the species. Maintenance of the community as a whole may then depend on a pattern or mosaic of microsites differing in ways affecting probabilities of survival in them for different species.

It is possible for two or more species populations to survive together with stable flow of their reproduction through a mosaic of microsites that are not differentiated (Skellam, 1951; Levin, 1974; Whittaker, 1975). The soil surface of the community may, however, be regarded as a mosaic of differentiated microsites, many occupied by plants, but some vacant though they are of sizes suitable for seedlings. (The mosaic concept is convenient, although plant microsites and open microsites are continuous with one another in the microsite pattern and differ in size with plant age and size). For communities subject to gap-phase process or succession following small-scale disturbance, microsites differ along time and disturbance axes, as well as with more stable soil characteristics and biological effects. Differentiation of microsites may be a major determinant of population regulation, coexistence and relative abundance of species (Whittaker, 1975; Whittaker & Levin, 1977).

Consider as a simplification a level, leached, sandy soil that is completely homogeneous and devoid of plants, a terrestrial biotope as a *tabula rasa*. On this, woody plants and grasses of different species establish themselves and modify the soil in ways that include differences in nutrient concentration and turnover. A complex pattern of soil nutrients may thus be produced, and this pattern would be further complicated by histories of past occupation of microsites by different species and by animal effects. Initial differentiation of the soil (which is more likely than complete homogeneity) would contribute to determination of the nutrient pattern, but is not necessary to obtain that pattern. Plant species differ in nutrient requirements and use (cf. Siccama *et al.*, 1970; Woodwell *et al.*, 1975; Whittaker *et al.*, 1979c). If two species differ in nutrient use, and especially in the particular elements limiting their growth, they may grow in close proximity without competitive exclusion (cf. Titman, 1976). Patterns of difference in nutrient availability plus differences in species responses to nutrient availability can then, in principle, provide microsite and niche differences for a considerable number of plant species.

Animals produce not only local fertilization but local disturbances creating vacant microsites. Plants of the savanna appear adapted to both grazing and fires that sweep the savanna every few years — few plants dead from either cause were noted. Both fires and grazing should, however, along with plant senescence and periodic drought and other factors, imply plant mortality producing open microsites, differing in their properties, in which different species reproduce.

A concept of the *Burkea* savanna is suggested. The community is rich, with about 70 perennial species per tenth hectare, plus a larger number of annuals than the 30 recorded by us in an unfavourable year. The perennials form the structure and determine the microsite pattern of the community without fully occupying the soil surface. Sites lacking perennial cover, together with sites vacated by plant mortality, provide a partly continuous, partly episodic supply of open microsites differing in ways affecting probabilities of germination and survival for different species. Differences in reproductive timing and dispersal mechanisms may permit survival in the community of more than one species dependent on a given kind of (or range of characteristics of) microsite. Population turnover and maintenance of a considerable number of perennial species through the microsite mosaic is thus possible. Differences in height, root depth, and relative requirements for different nutrients may permit adjacent plants to survive as they grow and their microsites overlap. A seedling may also establish itself on bare soil within the root area of an older plant; differences in root depths or other characteristics may permit these plants to survive in overlapping microsites. Differences in both seedling microsite requirements and adult plant characteristics may thus contribute to coexistence of species and to community diversity. Since the perennial plants do not fully occupy the soil surface, there are also microsites for the annuals. Populations of these turn over through microsites favourable to them in a manner similar to that of the perennials, but on different scales of time and microsite area and with marked year-to-year fluctuation.

Such relationships make possible coexistence of a large number of plant species — over 100 in the *Burkea* savanna — in an equilibrium condition. The plant species diversity and structural complexity of the community make possible the coexistence of a rich animal community while, in turn, effects of the animals, limiting plant dominance and increasing microsite heterogeneity, contribute to maintenance of the richness of the plant community (Whittaker, 1972, 1977a,b). Severe community-wide disturbance, or chronic disequilibrium and fluctuation (Connell, 1978; Huston, 1979) are not needed for the maintenance of richness in this community, although some communities may evolve to relative richness in the face of these (Grassle & Sanders, 1973). The African savannas are long influenced by man; fires were a normal part of the environment before man and were increased in frequency by man. Small-scale local disturbances by animals are also normal to the community. With allowance for the effects of fire, man, and other animals, the *Burkea* savannas are reasonably regarded as climax — self-maintaining communities that, although some fluctuation is normal to them, remain relatively consistent in mean species composition through periods representing several or many life-cycles for their organisms.

Microsite differentiation and within-community pattern are partly causes of each other — they are complementary. Balances of competing species populations and relative importances of species are determined by turnover through, and survival in, differing microsites. Some of these relationships may be amenable to research with natural communities of short-lived plants. Microsite differentiation, including biological effects, may be the key to maintenance of diversity in rich communities.

Acknowledgements

We thank B.J. Huntley and the South African Programme for Environmental Sciences of the CSIR, Pretoria, for support of the work at Nylsvley; the numerical and soil analyses at Cornell University were supported by National Science Foundation grant DEB 78–09340 for 'A Program of Research on Community Analysis'. The field work was based at, and assisted by the personnel and facilities of the South African Savanna Ecosystem Project in the Nylsvley Nature Reserve. G.K. Theron helped the study with plant taxonomy in the field and with interpretation of species-habitat relationships, and the staff at the National Herbarium, Pretoria, identified many voucher specimens at short notice. L.S. Olsvig-Whittaker was responsible for soil sampling and processing and for final manuscript review, and H.G. Gauch Jr, S. Singer, T. Mason, R.H. Westfall and G. Venter assisted with computer analysis. M.O. Hill shared many ideas with us. The field sampling team included J.W. Morris, G.K. Theron, R.H. Whittaker, L.S. Olsvig-Whittaker, M. Borthwick, S. Holmes, R. Manders, T. van Rensburg, N. van Rooyen, R.H. Westfall and E. Witkowsky. B.J. Coetzee assisted with sampling in the Kruger National Park.

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